SOYBEAN RESPONSES TO ELEVATED TEMPERATURE AND DOUBLED CO_2

By

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Abstract of Dissertation Presented to the Graduate School of the University of Florida in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy

SOYBEAN RESPONSES TO ELEVATED TEMPERATURE AND DOUBLED CO_2

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The atmospheric CO_2 concentration is projected to double and the air temperature is projected to increase by 1.5 to 4.5 °C in the next century. The objective of this study was to evaluate the effects of doubled CO_2 and elevated temperature on photosynthesis, respiration, transpiration, growth and development of soybean. Soybean (*Glycine max (L.) Merr.* c.v Bragg) was grown in eight sunlit, computer-managed and environment-controlled growth chambers. There were five levels of temperatures with maximum/minimum temperature at 48/38, 44/34, 40/30, 36/26, 32/22 and 28/18 °C at day/night, and two levels of CO_2, 350 and 700 μmol mol^{-1}. The experiments were conducted in 1993 and 1994 with different treatments.

Doubled CO_2 increased canopy photosynthesis by 50% and therefore increased total dry matter accumulation. Elevated temperature did not significantly reduce canopy photosynthetic rate at doubled CO_2 because the optimum temperature for

photosynthesis was raised and the leaf area index increased at elevated temperatures. Whole plant dark respiration rate increased as the treatment temperature increased. Elevated temperature also increased specific respiration.

Daily canopy evapotranspiration (ET) increased as the temperature treatment increased. ET decreased at doubled CO_2 because canopy resistance increased with increasing CO_2 concentration. Water use efficiency increased at doubled CO_2 and decreased at elevated temperatures. Both the increased crop leaf area and the increased foliage temperature at doubled CO_2 tended to offset reductions in ET resulting from elevated CO_2 treatment. The results indicated that crop water use may increase at elevated temperature and doubled CO_2.

Doubled CO_2 did not significantly affect vegetative or reproductive development, but elevated temperature increased growth duration from sowing to harvest. Seed yield was increased about 30% at doubled CO_2 due to an increase in seed number. Elevated temperature increased seed number up to a mean air temperature of 35 °C and sharply decreased it above 35 °C. Seed yield and seed size decreased, and percentage of shrunken seeds increased at temperatures higher than 36/26 °C.

These results indicate that the combined effects of doubled CO_2 and increased temperature would increase soybean yield in cooler regions. In warm tropical regions, doubled CO_2 and increased temperature together would decrease seed yield and quality, while increasing water use.

CHAPTER 1
LITERATURE REVIEW

Introduction

The atmospheric CO_2 concentration has been increasing and air temperature has increased about 0.5 °C during the last century (IPCC, 1990). Because of human activities, atmospheric CO_2 concentration is projected to double and air temperature is projected to increase 1.5 to 4.5 °C in the next century (IPCC, 1990). Climate changes are expected to impact crop production. Soybean is one of the major crops grown in the United States (FAO, 1992). The evaluation of the effects of doubled CO_2 and elevated temperature and their interactions could enable us to predict soybean productivity and plan crop production in the future.

Previous experimental results have shown that elevated CO_2 concentrations have positive effects on soybean physiology and seed yield and will be described in this chapter. However, few experiments have been conducted at temperatures higher than 36 °C. There is limited information about the effects of elevated temperature and the interactions between doubled CO_2 and elevated temperature on soybean physiological responses and seed yield.

Based on a long term experiment at a daytime maximum

temperature of 36 °C (Baker et al., 1989), soybean plants appear to be more tolerant to high temperature during the reproductive phase than other main summer crops, such as cotton (Reddy et al., 1991a, 1991b) and rice (Baker et al., 1992a, 1992b). Reproductive growth of both rice and cotton was severely affected and yield was sharply decreased at elevated temperature in these studies. It is hypothesized that soybean reproductive growth would be adversely affected because of infertility and seed growth problems caused by elevated temperature; that negative effects of elevated temperature on dry matter accumulation of soybean plants might be balanced by the positive effects of doubled CO_2; and that yield might be decreased (but not as sharply as rice or cotton) if the air temperature increases in the future.

The objectives of this study were to evaluate the effects of temperature higher than 36 °C at 700 μmol CO_2 mol^{-1} level on following processes: leaf and canopy photosynthesis, whole plant nighttime respiration, leaf stomatal conductance, leaf temperature, canopy evapotranspiration and water use efficiency. The objectives were also to quantify the effects of elevated temperature at 700 μmol CO_2 mol^{-1} on soybean growth and development, dry matter accumulation and partitioning, leaf area, specific leaf weight, seed growth rate and yields.

Climate Change

The Evidence of Climate Change

The solar radiation absorbed by the Earth's surface and atmosphere is balanced at the top of the atmosphere by outgoing radiation at infrared wavelengths. Some of the outgoing infrared radiation is trapped by the naturally occurring greenhouse gases, aerosols, particulate matter, water vapor and clouds. Greenhouse gases such as water vapor (H_2O), carbon dioxide (CO_2), ozone (O_3), methane (CH_4), nitrous oxide (N_2O), carbon monoxide (CO), nitrogen oxide (NOx), reactive nitrogen (NOy) and halocarbons of different types, such as chlorofluorocarbon (CFCs), hydrochlorofluorocarbon (HCFCs) and hydrofluorocarbon (HFCs) absorb some of the infrared radiation emitted from the earth's surface and re-emit it in all directions (IPCC, 1994). The effect of this is to warm the surface and the lowest region of the atmosphere, the troposphere. The atmosphere's chemical composition is an important determinant of its thermal budget.

The modern era of climate-related atmospheric chemistry began in 1958 when C. D. Keeling commenced his highly precise and accurate measurements of carbon dioxide at Mauna Loa, Hawaii. It was found that CO_2 concentration had increased from 315 μmol mol^{-1} in 1958 to 350 μmol mol^{-1} in 1988. Keeling et al. (1989, 1995) described a set of observations that span the Central Pacific and showed the exponential rise of CO_2. The

increase in atmospheric CO_2 concentration was 0.83 μmol mol^{-1} yr^{-1} during the 1960s, 1.28 μmol mol^{-1} yr^{-1} during the 1970s, and 1.53 μmol mol^{-1} yr^{-1} during the 1980s. The current rate of increase of CO_2 concentration is 1.53 μmol mol^{-1} yr^{-1} or close to 0.4% per year (Boden et al., 1991, Conway et al., 1994). The sources of atmospheric CO_2 are mainly from the burning of fossil fuels (coal, oil, natural gas), cement production, and deforestation.

The record of the atmospheric CO_2 concentration at high latitudes can be extended back in time by analyzing the composition of air trapped during the formation of glacial ice in Greenland and Antarctica. The conversion of snow into ice takes at least a decade and the dating of the past by analyzing trapped air bubble samples can not be very accurate. This method, however, gives good relative data. The CO_2 concentration in 1740 was about 277 μmol mol^{-1}. About 80.7 Gt of carbon were added to the atmosphere in the 218 years between 1740 and 1958 (Neftel et al., 1985, Friedli et al., 1986).

A joint French-Soviet team extended the record of atmospheric carbon dioxide concentration farther back into glacial times by using an ice core from Vostok, Antarctica. Their results show that during times of maximum ice coverage in the Northern Hemisphere, atmospheric CO_2 concentrations reached a minimum value of about 180 μmol mol^{-1} (Delmas et al., 1980, Barnola et al., 1987). During the prior interglacial

warm period, the atmospheric CO_2 concentration reached 290 μmol mol^{-1}, a level comparable to the preindustrial concentration.

Methane is a strong infrared absorber. It is the most abundant reactive trace gas in the troposphere and determines the atmospheric concentrations of ozone and hydroxyl radicals. The reaction of methane with hydroxyl radical (OH) in the stratosphere results in the production of water vapor ($OH + CH_4 \rightarrow CH_3 + H_2O$). Chemical reactions involving CH_4 in the troposphere can lead to ozone production,

CH_4 (+OH) -> CH_3 (+O_2) -> CH_3O_2 (+NO) -> CH_3O (+O_2) ->

HCHO (+hv) -> HCO (+O_2) -> CO (+OH) -> CO_2

NO_2 (+hv) -> NO + O (+O_2) -> O_3

Both tropospheric ozone, especially in the upper troposphere, and stratospheric water vapor are significant greenhouse gases. Although methane has a lifetime about 12-17 years in the atmosphere, the final oxidation of CH_4 produces CO_2 which is also a greenhouse gas. Methane data measured from ice core samples (Stauffer et al, 1985; Stauffer et al., 1988; Raynaud et al., 1988; Craig and Chou, 1982) and observed in recent decades (Dlugokencky et al., 1994) show that the CH_4 concentration is continuously increasing. Globally, methane increased by 0.8% yr^{-1} or 13 nmol mol^{-1} over the decade beginning in 1983 (IPCC, 1994).

Nitrous oxide (N_2O) is the primary source of the oxides of nitrogen oxides (NOx includes NO and NO_2) in the

stratosphere and play a critical role in controlling the abundance of lower stratospheric ozone:

$NO + O_3 \rightarrow NO_2 + O_2$

$NO_2 + O \rightarrow NO + O_2$

Nitrous oxide can contribute to stratospheric O_3 depletion by producing NOx as it breaks up in the stratosphere. Nitrous oxide is an infrared absorber. NOx is involved in the ozone formation in photochemical 'smog' in the lower troposphere:

$HO_2 + NO \rightarrow OH + NO_2$

$NO_2 + h\nu$ (<0.38 μm) $\rightarrow O + NO$

$O + O_2 + M \rightarrow O_3 + M$

The lifetime of N_2O in the atmosphere is about 120 years (IPCC, 1994). The annual growth rate of N_2O has been 0.2 to 0.3% in recent decades (Rasmussen and Khalil, 1986).

Halocarbons containing fluorine, chlorine and bromine are significant greenhouse gases. One CF_2Cl_2 molecule has the approximate equivalent "radiative forcing" of 15,800 CO_2 molecules at current concentrations of these gases in the atmosphere (IPCC, 1990). Inert in the troposphere, halocarbons undergo photodecomposition when they reach the stratosphere, producing compounds and free radicals that destroy stratospheric ozone, such as:

$Cl + O_3 \rightarrow ClO + O_2$

$Br + O_3 \rightarrow BrO + O_2$

The annual atmospheric increase in the concentration of halocarbons is from 2% to 7%, varying with different compounds

(IPCC, 1994).

Ozone is a short-lived constituent in the lower atmosphere (<12 km) that is produced when photolysis of nitrogen dioxide occurs in the presence of hydrocarbon:

$OH + RCH_3 \rightarrow H_2O + RCH_2$

$RCH_2 + O_2 \rightarrow RCH_2O_2$

$RCH_2O_2 + NO \rightarrow RCH_2O + NO_2$

$RCH_2O + O_2 \rightarrow RCHO + HO_2$

$HO_2 + NO \rightarrow OH + NO_2$

$NO_2 + hv$ (<0.38 um) $\rightarrow O + NO$

$O + O_2 + M \rightarrow O_3 + M$

A principal component of smog, ozone has become a regional pollutant in many parts of the world. Increases in concentrations of lower-level ozone have also been measured at remote sites. No trend was detected at the south pole (Oltmans and Komhyr, 1986). The formation of ozone is closely related to the emission of non-methane hydrocarbon, NOx and CO. Ozone can also be transported into the troposphere from the stratosphere. Changes in tropospheric ozone concentration are highly spatially variable, both regionally and vertically, making assessment of global long-term trends extremely difficult. On the other hand, decreases in stratospheric ozone have occurred since the 1970s (IPCC, 1994). The ozone loss occurs at altitudes between about 14 to 24 km and it is mainly caused by the chlorine and bromine compounds released in the stratospheric decomposition of halocarbons. The decrease of

ozone in the stratosphere may let more ultraviolet radiation penetrate into the lower atmosphere and may be harmful to human beings, animals and plants. However, the ultraviolet radiation contributes little directly to the total global radiation balance (Allen, 1994c, 1994d). Meanwhile, significant questions remain with regard to the influence of ozone losses on stratospheric temperature (IPCC, 1994). The loss of ozone in the lower stratosphere over the past 15 to 20 years has led to a globally averaged radiative forcing of about -0.1 W m^{-2}. This negative radiative forcing represents an indirect effect of CFCs and halons which may have partially offset their direct warming effect. However, because the pattern of stratospheric ozone loss is not spatially uniform (it occurs mainly at mid-latitudes and polar regions), the amount of offsetting is difficult to estimate.

Research concerning the possibility that rising levels of atmospheric CO_2 could cause global temperature to increase via the greenhouse effect started in the 1950s (Plass, 1956, 1959: Kaplan, 1960; Moller, 1963). The CO_2 concentrations and surface temperatures derived from the deuterium content of Vostok ice cores from Antarctica show that a close relationship has existed between global CO_2 concentration and air temperature over the past 160,000 years. Hansen and Lebedeff (1987, 1988) and Jones, P. D. et al. (1986) analyzed temperature data over the past 108 years. Their data show that the feature common to various compilations of temperature

records: all agree on a warming of about 0.5 °C over the past century. The change in air temperature is related to that of CO_2 and methane. Another independent method for providing evidence of changes in temperature was used by Lachenbruch and Marshall (1986), who examined the variation of temperature with depth in the permafrost region on the North Slope of Alaska. The ground is permanently frozen to a depth of several hundred meters and subsurface temperatures remain undisturbed. In the absence of water movement, heat is carried out of the earth solely by thermal conduction. Lachenbruch and Marshall found that the observed subsurface temperature was consistently 2 °C to 4 °C warmer than that obtained by upward extrapolation of the thermal gradient. This observation is consistent with a global average warming of 0.5 °C owing to the amplification of postulated greenhouse warming at high latitudes.

An estimate of global mean sea level change during the last 100 years indicates a rate of rise of 1.0-2.0 mm yr^{-1} based on at least sixteen studies of tide-gauge data (Gornitz et al., 1982; Gornitz 1993; Peltier and Tushingham, 1989). The agreement among these independent data analyses, in spite of the diversity of sampling strategies and data processing techniques, lends support to the notion that the observed sea level rise represents a true change. Although the see level observations are subject to large uncertainties due to geographical distribution, vertical land movement, atmospheric

and oceanographic effects, they are consistent with a warming of 0.5 °C. Close relationships exist among changes of global sea level, global air temperature, global CO_2 and methane concentrations over the past 160,000 years.

The method used for determining CO_2 in ice cores is mainly the direct measurement of trapped air in ice core (Barnola et al., 1987). Their method is based on crushing the ice under vacuum without melting, expanding the gas released during the crushing in a pre-evacuated sampling loop, and analyzing the CO_2 concentration by gas chromatography. The determination of air temperature from the present to 160,000 years before the present is based on the measurement of deuterium or $\delta^{18}O$ in ice cores (Jouzel et al., 1987). Over a large range of temperatures (-20 to 55 °C), there is a linear relationship between the annual average surface temperature and the ice core deuterium content. The temperature record over the last climate cycle (160,000 years) is indirectly calculated (Jouzel et al., 1987).

Observations of $^{13}C/^{12}C$ and O_2/N_2 are used for carbon budget assessment. The methods based on ^{13}C measurements exploit the fact that the $^{13}C/^{12}C$ ratio in fossil fuels and terrestrial biomass is less than that in the atmosphere. There has been a decline in the $^{13}C/^{12}C$ ratio of atmospheric CO_2 over the last century (Keeling et al., 1989). This $^{13}C/^{12}C$ ratio change propagates through the global carbon cycle, causing isotopic ratio changes in the ocean and the terrestrial carbon

reservoirs.

Difference of opinion exists about the possibility of climate change. Rasool and Schneider (1971) reported that both global CO_2 and aerosol in the atmosphere have increased, and that an increase by only a factor of four in global aerosol background concentration may be sufficient to reduce the surface temperature by as much as 3.5 °C. This would lead to a surface temperature cooling instead of warming. Yarnal (1992) pointed out that there exist within-year, year-to-year and decade-to-decade climate variations. Regardless of the regional impact of global warming, climatic variability will continue to be a constant joy to future generations. Karl (1992) suggested that we can not be sure about the exact magnitude of the average global mean temperature increase because of inadequate spatial and temporal sampling and changes in observation methods. However, these alternate opinions have not been widely accepted.

The Prediction of Climate Change

The foregoing observations and research results clearly show that the composition of the earth's atmosphere, such as concentrations of CO_2, methane, nitrous oxide and halocarbons, and climatic parameters, such as the air temperature, have been changing since the beginning of the industrial revolution. However, many other factors are involved in the whole system.

The key processes in the global carbon cycle include: the exchange of CO_2 between the atmosphere and ocean; the exchange of CO_2 between surface waters and long term storage in the deep ocean; the net release or uptake of CO_2 from changes in land-use practices; the photosynthetic uptake of CO_2 by land plants; the transfer of their carbon into long-term storage in wood and soils; the response of these processes to changing CO_2 and climate, and the release of CO_2 back to the atmosphere through plant and soil respiration; and the CO_2 emission rate in different countries of the world. The carbon cycle also includes chemical reactions in the atmosphere. The dynamics of CO_2 concentration estimates is simulated on the basis of assumptions of different CO_2 emission scenarios in the future. Stabilization of the current global emission of CO_2 would not lead to stabilization of CO_2 concentrations until 2100, but CO_2 levels would be expected to reach about 500 μmol mol^{-1} by the end of 21st century in this scenario (IPCC, 1994). In general, CO_2 levels would be expected to double by the 21st century in this scenario (Trabalka, 1985, IPCC, 1994).

Several general circulation models (GCM) have been developed to model climate changes by different research institutes, such as the Geophysical Fluid Dynamics Laboratory (GFDL, Manabe and Wetherald, 1987), the Goddard Institute of Space Science (GISS, Hansen et al., 1984), the National Center for Atmospheric Research (NCAR, Washington and Meehl, 1984), the Oregon State University (OSU, Schlesinger and Zhao, 1989),

and the Meteorological Office of the UK (UKMO). These models include atmospheric motions, the thermodynamics, hydrodynamics, and the conservation of momentum, mass and energy. Rectangular grid or spectral methods are used to describe the vertical and horizontal exchanges between the adjacent columns and layers (Henderson-Seller and Verstraete, 1987). Models do relatively well in representing global average conditions, latitudinal variation of climate, range of seasonal change, and wintertime temperature, but they do poorly in representing longitudinal and regional variations of climate, summertime temperatures, precipitation, and surface hydrology (Report of the DOE multi-laboratory climate change committee, 1990). The estimated increase of global average temperature resulting from a doubling of the atmospheric CO_2 for various versions of the five models (GFDL, GISS, NCAR, OSU, UKMO) show that the range of temperature increase over land areas is generally from 1.5-4.5 °C, with little agreement among models on the distribution of these changes (Report of the DOE multi-laboratory climate change committee, 1990). It has been generally accepted that there will be global warming by as much as a few degrees through the next century, with amplified warming in polar regions as snow cover and sea ice melt back and increased evaporation occurs especially in summer. Simulation results also suggest that there will be a sea level rise of tens of centimeters, moderate warming at low latitudes, increased summer drying of continental interiors

and more frequent hot summer days.

These climate changes might directly or indirectly affect humans, animals and plants. They would perturb the agricultural ecosystem via effects of elevated CO_2 on different species of plants. Elevated temperature would increase evapotranspiration from plants and evaporation from land or water surfaces, therefore increasing the amount of water required for plant production. Potential production would decrease in warm regions and increase in cool regions. The plant species would shift in some regions as the water supply changes and air temperature rises. Some cropping systems such as the corn belt would shift further to the north. Insects and diseases might also change because of the modification of the ecosystem. The world population and demands for fiber and food are increasing, therefore, it is very important to know the effects of potential climate change on plant growth.

Soybean Responses to Elevated CO_2 and Temperature

Current Research Approaches

Field techniques for exposure of plants and ecosystems to elevated CO_2 and other trace gases have been reviewed by Allen et al. (1992). Before 1980, most studies on the effects of elevated CO_2 concentration were carried out in controlled environment facilities including leaf cuvettes, whole-plant growth chambers and greenhouses. As computer technology is

widely used in control systems, current systems used for this research have been greatly improved. The techniques that have been used can be briefly summarized as follows.

Portable photosynthesis systems

These systems are mainly used for measuring single leaf gas exchange (Hileman et al., 1992a; Ziska et al., 1995). The most widely used portable systems are LICOR (USA) and LPI (England). Photosynthesis, respiration, transpiration, and conductance or resistance to gas exchange can be automatically measured for single leaves. The instrument is manipulated with software and is convenient to operate (LICOR, 1987). The measurements can be conducted with controlled light flux density, air temperature and CO_2 concentration. The data can be downloaded into a computer and the results can be easily processed. However, the system is sensitive to air humidity and air temperature, therefore, the measurements must be carefully made.

Portable field chambers

Portable field chambers have been designed for short term gas exchange measurement (Jones et al., 1982; Boote et al., 1984; Pickering et al., 1993). One typical portable chamber was approximately one m^3 in volume and was constructed using an aluminum frame covered with Mylar film. A fan was used to circulate the air within the chamber and CO_2 measurement could be conducted by using an infrared gas analyzer or the portable LICOR system. These chambers can be used for canopy CO_2

exchange (water vapor exchange with LICOR) measurement (Boote et al., 1980; Garrity et al., 1984; Boote et al., 1985). A disadvantage is that only short term transient measurements are possible because temperature and humidity increase rapidly over time.

Open-top ventilated chambers

Open top chambers, as described by Hogsett et al. (1985) and Heagle (1989), have been used to expose potted plants, annual crops, and trees to a variety of airborne pollutants and CO_2. The system can recirculate part of the input air (Drake et al., 1989) and can be operated with computerized control and data acquisition systems. The actual top openings can have different sizes (25%, 50%, 75% of chamber diameter) and use different angles (30, 45, 60°) of elevation. Decreasing the size of the open top and decreasing the angle of the frustrum minimizes turbulent incursion losses through the outlet of the open-top chambers (Baldocchi et al., 1989). Allen et al. (1992) pointed out that air flow through an open-top chamber could be influenced greatly under high wind speed conditions. The variability of CO_2 flow through the open-top chambers under windy conditions is the greatest. Rogers et al. (1984) used open-top chambers. A high rate of ventilation was required to maintain the inside temperature and humidity close to that of the outside air. Open-top chambers provide enriched CO_2 condition but inside plant growth differs from that on outside because of the micrometeorological conditions.

Outdoor, sunlit, environment-controlled chambers

Controlled-environment chambers are based on closed system. A good example is the Soil-Plant-Air-Research (SPAR) unit used in Gainesville, Florida (Jones et al., 1984b; Pickering et al., 1994). The SPAR chambers were also used in Oregon, Mississippi State University, and Clemson University. The SPAR chambers used at the University of Florida were greatly improved over time by using computerized control systems. They allow direct measurement of the CO_2 exchange rate. The transpiration rate was measured by collecting condensate from air conditioning cooling coils. The system was controlled by running real time software, measuring chamber air CO_2, temperature and humidity etc., and actuating control devices using feedback from measured data. Chamber air was circulated through the canopy from the top to bottom and then through a heat exchange duct. Measurements were summarized and recorded at five minute intervals (Jones et al., 1984b). The chambers were successfully used to measure photosynthesis, respiration and transpiration as a function of CO_2 concentration, light, and temperature (Allen et al., 1985; Baker et al., 1990a; Reddy et al., 1991a, 1991b). There are disadvantages such as chamber effects, limited replications, and the expense for each unit. However, the daily cost for the use of CO_2 was greatly reduced.

Free-air CO_2 enrichment

The free-air CO_2 enrichment (FACE) approach does not use any chamber wall or top restriction, rather CO_2 is supplied in the open field by using a pipe ring. With this method, a distribution system was designed for area-source emission, upwind vertical vent pipe emissions, and a combination of area-source and upwind vertical vent pipe distribution systems. The environmental condition in FACE experiments is the same as that in a natural ecosystem. Plant growth is also the same as that under field conditions except for elevated CO_2. However, field wind speed and direction varied from hour to hour and day to day and required considerable work to maintain a stable CO_2 concentration in the field (Nagy et al., 1992). The use of the FACE system requires periodic three-dimensional sampling of CO_2 in order to adjust the distribution of emission holes (Hileman et al., 1992b). An advance in FACE technology by Brookhaven National Laboratory using closely controlled release of pre-diluted CO_2 through a circular array of vertical vent pipes represents a new approach in CO_2- vegetation effect research. Another advantage of the FACE system is that there is no reduction of PAR and UV-B radiation. The wind flow, turbulence, temperature and humidity are natural. Soil and water patterns are not disturbed. However, the cost for CO_2 is several times as much as that for SPAR or open-top chambers (Kimball, 1992).

Greenhouses and tunnels

Greenhouses are constructed with frame and highly transparent glass or Mylar. The cost for building the system is relatively low. The temperatures and CO_2 concentrations are, in general, roughly controlled. Greenhouses allow experiments to be done during cold seasons. Greenhouses provide a large area that allows for more replicates. However, the light intensity inside the greenhouse is lower than that outside. The humidity is usually not controlled. The effect of water stress, in many cases, has been underestimated in comparison with field conditions (Kimball, 1986). In greenhouses, water and nutrients are well supplied. This creates differences from the field conditions. Results from greenhouses may not be extrapolated or compared with those from field experiments.

Tunnels are, in principal, similar to greenhouses, but air in each tunnel is usually ventilated linearly along its length. Therefore, tunnels can establish CO_2 and/or temperature gradients along one direction for interaction studies. However, there are greenhouse chamber effects in tunnels. Plant growth in tunnels may differ from that in the field because the micrometeorology in tunnels is different from that outside and irradiance is less.

CO_2 Exchange

Photosynthesis

Plant carbon exchange is directly coupled with carbon dioxide concentration of the atmosphere in which the plants are exposed. Brun et al. (1967), Egli et al. (1970), Havelka et al. (1984), Jones et al. (1984a, 1985a, 1985b), Rogers et al. (1984), Sionit et al. (1984, 1987b), Acock et al. (1985), Campbell et al. (1988) and Ryle et al. (1992a) reported that leaf and canopy photosyntheses of soybean were greatly increased at elevated CO_2 concentration. Valle et al. (1985) found that high CO_2-grown plants had a higher leaf maximum photosynthesis rate, while their CO_2 and light compensation points, and photorespiration were lower. The higher productivity of soybean plants at elevated CO_2 is attributed to a higher CO_2 exchange rate and a larger green leaf area, which were due to long-term elevated CO_2 exposure. Leaf photosynthesis varied with leaf age. Photosynthesis was enhanced to the greatest extent in middle-aged leaves at elevated CO_2; very young leaves exhibited little enhancement, and net photosynthesis in the oldest leaves was depressed by elevated CO_2 (Kelly et al., 1991).

Photosynthesis of C_3 plants generally increases with increasing CO_2. Sharkey (1994) suggested that photosynthesis may be limited at elevated CO_2 by ribulose bisphosphate carboxylase limitation, ribulose-1,5-bisphosphate regeneration limitation, and end-product synthesis limitation. Altered

carbon dioxide concentration may affect gene expression, the effect of increased CO_2 concentration on gene expression of terrestrial plants is likely to be mediated through changes in metabolite balance (Spalding, 1994). Sinclair (1989) reviewed the relationship between leaf nitrogen and photosynthesis, and showed that leaf photosynthesis increased with increasing nitrogen content. This illustrates the relationship between soybean assimilation and rubisco protein content at ambient CO_2.

Allen (1979), Kimball (1983), Cure and Acock (1986), Allen (1990, 1994b) reviewed plant responses to elevated CO_2. In general, C_3 plants have larger response to doubling CO_2 than C_4 plants. On the average, leaf photosynthesis of C_3 plants is increased about 50%. Increase of net photosynthesis with CO_2-enrichment has sometimes resulted in end-product inhibition (Hesketh et al., 1983).

A lot of attention has been focused on photosynthesis acclimation. Some reports show that plant photosynthesis measured at ambient CO_2 decreased after the plants had long term exposure to elevated CO_2 (Kramer, 1981, Peet et al., 1986). Jones et al. (1985a) reported that soybean CO_2 exchange rate depended on the current CO_2 concentration rather than CO_2 history, that the plants had been exposed previously. They reported an upward acclimation of soybean canopy photosynthesis. The upward acclimation may be indirectly the result of larger leaf area index, which was caused by long

term elevated CO_2 exposure. Kelly et al. (1991) conducted a CO_2 switching experiment and suggested that photosynthesis at low CO_2 was limited by CO_2 regardless of the development environment of the leaf, whereas photosynthesis at high CO_2 was limited by the developmental characteristics of the leaf. Specific leaf weight was increased when plants were moved from ambient CO_2 into doubled CO_2 for long term treatment. Ryle et al. (1992a) found that white clover leaves developed in 680 μmol mol^{-1} CO_2 had lower photosynthetic rate than those developed in ambient CO_2 when both are exposed to the ambient CO_2. Allen (1994b) summarized five types of acclimation responses from different species of plants: 1) decreased initial slope (α) and decreased maximum photosynthesis rate (A_{max}); 2) decreased α with converging A_{max}; 3) same α with increased A_{max}; 4) increased α and increased A_{max}; 5) same α and same A_{max}. Therefore, acclimation may vary with plant species.

Respiration

In the estimation of the effects of CO_2 and elevated temperature on respiration, different methods for separating maintenance and growth respiration have been used. Direct measurement of CO_2 exchange in the darkness is the main method to estimate total dark respiration. The separation of growth and maintenance respiration is difficult. Different valuable methods have been developed, however, each method has shortcomings.

The regression method is based on the relationships

between respiration, photosynthesis, and accumulated dry matter. The calculations include:

McCree (1970): $R=kP+cW$, $g=(1-Y_G)/Y_G$, $m=c/(1-k)$

Hesketh (1971): $dW/dt = Y_G(P-mW)$

Fernandez (1977): $R/W = g/(dW/dt) + m$

where: R = daily total respiration

P = daily gross photosynthesis

W = dry matter of living tissue

Yg = growth conversion efficiency

k and c = constant

g = growth respiration coefficient

m = maintenance respiration coefficient

The equations give good estimation of growth and maintenance respiration. However, the parameters in the equations may vary naturally during crop ontogeny and rely on photosynthesis measurement and the environmental conditions. Even when whole plant carbon balance is assumed to be zero, there are new leaves replacing the old ones and this implies that measured respiration is not completely attributable to maintenance processes. Accurate estimation of dW/dt is also difficult.

The starvation method (Irving and Silsbury, 1987) has been used to estimate the minimal maintenance requirement. The plants are continuously kept in the dark for 40 hours. In this case, the growth is assumed to have stopped because the substrates have been depleted. The respiration rate at this time is considered to be the maintenance respiration. The

difference between the respiration rate at the beginning of the dark period and the rate at the end of the dark period is estimated as growth respiration. It is a practical method. There is also a shortcoming. After a long dark period, meristematic activity continues forming new structural phytomass, thus growth respiration is not really zero; the duration of the dark period to reach the stable state depends on the plant size because the larger plants may take a longer time; different durations of dark period may cause inaccuracy. The mature tissue method (Wilson 1975, 1982) is very similar to starvation method, but does avoid the continuing growth respiration of meristematic regions.

Based on biochemical knowledge, Penning de Vries (1975) provided a rather elaborate first estimation: the theoretical method. The calculation is based on the biochemistry associated with growth and maintenance processes. Maintenance respiration is calculated from the CO_2 respired for the turnover of labile compounds, such as lipids, proteins, and membranes. The accuracy is limited by the gaps in our knowledge of underlying processes and their rates in vivo, and limited by the cellular physiology data. The accuracy may vary with the actual biochemical pathways taking place in situ. There might be small errors of the theoretical assumption that could cause errors of growth and maintenance respiration calculation.

Amthor (1991) suggested that both elevated CO_2 and

elevated temperature might have direct or indirect effects on plant respiration metabolism. Plants treated with elevated CO_2 increased dark respiration on a ground area basis but decreased specific respiration on a dry matter basis (Baker et al., 1992c). High specific respiration was associated with high nitrogen concentration in the plants. Maintenance respiration was almost the same under both ambient and doubled CO_2 for rice (*Oryza sativa* L.) (Baker et al., 1992c). Gifford et al. (1985) found that growth of wheat (*Triticum aestivum* L.) in high atmospheric CO_2 was associated with up to 45% reduction in respiration by both root and whole plants, but elevated CO_2 did not decrease the respiration for Mung bean (*Vigna radiata* L.) and sunflower (*Helianthus annuus* L.) plants. Ziska and Bunce (1994a) found direct effect of CO_2 on leaf respiration on a dry weight basis for herbaceous perennial. No inhibition of respiration by CO_2 was observed at the highest growth temperature (30 °C) in herbaceous perennial (*Dactylis glomerata* L.) and alfalfa (*Medicage sativa* L.). It seems that CO_2 inhibition of respiration is greatly reduced at relatively high temperatures.

Other research showed that the CO_2 effect on growth and maintenance respiration was different. Ziska and Bunce (1994a) reported that growth respiration was reduced at 700 μmol mol^{-1} CO_2, and that maintenance respiration decreased at doubled CO_2 only under low temperature (15/20 °C) for herbaceous perennial (*Dactylis glomerata* L.) and alfalfa (*Medicage sativa* L.).

Thomas and Griffin (1994) found that the maintenance respiration coefficient increased 34% with 710 μmol mol^{-1} CO_2 for soybean leaves, whereas the growth coefficient was not significantly affected. The range in maintenance respiration was related to a 33% increase in leaf total nonstructural carbohydrate concentration. The results varied with species, thus further research is necessary for accurate conclusions on CO_2 effects on respiration.

Evapotranspiration and Water Use

Transpiration and stomatal conductance was studied as early as the 1940s. Van den Honert (1948) suggested a useful evapotranspiration equation:

$$LE = (\rho_a * C_p/\gamma) * \{(e_1-e_2)/(r_a+r_b)\}$$

where LE is the latent heat flux, ρ_a is the density of air, C_p the specific heat of air at constant pressure, and γ the psychometric constant, (e_1-e_2) is the gradient of water vapor pressure between the substomatal cavities of the leaf and the air outside the leaf, r_a and r_b are the resistance exerted by the stomata through which the vapor must pass to enter the air and by the leaf boundary layer, respectively.

The Penman-Monteith model is another important evapotranspiration equation (Monteith, 1965). This equation allows consideration of cases of either optimal or limited water supply, and it successfully estimates evapotranspiration from crops and forests (Rosenberg et al., 1983).

Stomatal opening was found to be decreased by elevated CO_2 concentration, and transpiration rate was therefore decreased (Gaastra, 1959; Akita & Moss, 1972; Kriedemann et al., 1976). It was also reported that leaf temperature was increased as transpiration was decreased by elevated CO_2 concentration (Gaastra, 1959). Doubling CO_2 concentration increases leaf temperature from 1 to 3 °C, depending on species and the weather (Idso et al., 1986, 1987; Choudhury et al., 1986; Kimball et al., 1992). The degree of temperature rise differs among species apparently because their stomata respond to CO_2 differently. Havelka et al. (1984), Acock and Allen et al. (1985), Jones et al. (1985a, 1985c) and Sionit et al. (1984) reported leaf stomatal conductance was decreased with increased CO_2. This is one reason why canopy transpiration decreases and water use efficiency increases (Jones et al., 1984a, 1985a). There is quantitative relationship between transpiration and conductance/resistance. Jones et al. (1984a) reported that canopy resistance of soybean at 800 μmol mol^{-1} CO_2 was 1.6 times that of the 330 μmol mol^{-1} CO_2 treatment. Cure (1985) reviewed 21 experiments and computed an increase of 51% in stomatal resistance. Kimball and Idso (1983) reviewed nine CO_2 enrichment experiments and calculated a 34% average reduction of leaf transpiration caused by doubling CO_2. Jones et al. (1985d) found that under 660 μmol mol^{-1} CO_2, soybean canopy transpired about 10% less water over the season than did the ambient CO_2

canopies. It was also found that whole chamber evapotranspiration was reduced 18%-27% for prairie grass (Bremer et al., 1994). Elevated CO_2 increased water use efficiency (WUE) and WUE depended on current CO_2 concentration rather than long-term CO_2 concentration as demonstrated in CO_2 switching studies by Jones et al. (1985a). Water use efficiency of rice canopies treated with elevated CO_2 was also found to be increased (Baker et al., 1990b). Allen et al. (1985) concluded that both the increased crop leaf area and the increased foliage temperature at doubled CO_2 tend to offset reductions in crop transpiration that might be expected from elevated CO_2. If global temperature rises with increasing CO_2, crop water use may actually increase.

Plant Growth, Metabolites and Enzymes

Acock and Allen (1985), Acock and Pasternak (1986) and Acock (1990) reviewed the growth responses of crops to elevated CO_2. There was little CO_2 effect on phenology, such as flowering and maturity dates (Cooper and Brun 1967; Allen et al. 1990). But the responses varied with crop species. Baker et al. (1990a) reported that elevated CO_2 accelerated rice development and reduced total growth duration. Soybean main stem development was not affected by elevated CO_2 (Jones et al., 1984a) or slightly increased (Allen et al., 1990).

Leaf area was significantly increased by elevated CO_2 (Cooper and Brun, 1967; Imai and Murata, 1976; Morison and

Gifford, 1984; Rogers et al., 1984; Allen et al., 1990). The increase of leaf area is enhanced by higher temperature and leaf area increase is proportional to leaf dry matter increase. Elevated CO_2 also increased specific leaf weight (Cooper and Brun, 1976; Sionit et al., 1982; Morison and Gifford, 1984; Rogers et al., 1984; Allen et al., 1990). The increase of specific leaf weight is positively correlated with higher density and number of layers of palisade mesophyll cells (Thomas and Harvey, 1983; Vu et al., 1989) and increased total non-structural carbohydrate in the leaves (Allen et al., 1988, Vu et al., 1989). The leaves of soybean plants grown in 800 μmol mol^{-1} CO_2 were 50% denser than those grown in 330 μmol mol^{-1} CO_2 (Acock and Allen, 1985). Epidermal cells remained constant in size across CO_2 concentration within a species (Thomas and Harvey, 1983).

Elevated carbon dioxide significantly increased total plant dry matter accumulation (Cooper and Brun, 1967; Hardman and Brun, 1971; Finn and Brun, 1982; Jones et al., 1984a; and Rogers et al., 1984; Baker et al., 1989; Allen et al., 1991). The range of dry matter increment varies with plant species and CO_2 concentrations. In both soybean and maize, the largest percentage increase in dry matter was for roots, a smaller increase to stems, and the smallest increase to leaves (Rogers et al., 1983). In general, plant height, number of nodes and branches were also slightly increased. At elevated temperature, root-to-shoot ratio was increased for several

crops (Imai and Murata, 1976; Sionit et al.,1982). Mauney et al. (1992) reported that final harvest dry matter of cotton (*Gossypium hirsutum* L.) was increased by 20% to 39% at 550 μmol mol^{-1} CO_2 concentration, but root biomass was increased by 85% for one variety.

On the average, the yield increased by 33% for doubling of atmospheric CO_2 concentration for C_3 crops (Kimball, 1983). Carbon dioxide enrichment from ambient to doubled concentration increased yield mainly by increasing pod or seed number for soybean (Cooper and Brun, 1967; Havelka, 1984; Sionit et al., 1987b; Baker et al., 1989), and by increasing the number of panicles per plant for rice (Baker and Allen, 1993a). Elevated CO_2 increased non-structural carbohydrates at normal temperature, but it increased structural carbohydrates only at high temperature. Therefore, harvest index could be increased by elevated CO_2 only at normal temperatures (Acock and Pasternak, 1986).

Elevated CO_2 can increase many metabolite levels. Total nonstructural carbohydrates, soluble sugar (reducing sugars, sucrose) and starch concentration of leaves were increased at elevated CO_2 (Ackerson et al., 1984; Allen et al., 1988; Havelka et al., 1984; Vu et al., 1989). The dry matter of nodules and plant total nitrogen were increased for soybean although nitrogen concentration in leaves was slightly decreased (Finn and Brun, 1982; Allen et al., 1988; Vu et al., 1989). The CO_2 effects on concentration of chlorophyll

differed among reports (Campbell et al., 1988; Havelka et al., 1984; Allen et al., 1988; Vu et al., 1989).

Bowes (1993) reviewed rubisco responses to elevated CO_2. Down-regulation of rubisco at elevated CO_2 has been reported in many species, and a number of species show either no decline or an increase in rubisco under elevated CO_2. Ribulose 1,5-bisphosphate carboxylase and oxygenase (Rubisco) activity showed no response to elevated CO_2 for soybean plants (Campbell et al., 1988; Vu et al., 1989). The amount of Rubisco protein was constant. It seemed that the higher photosynthesis at elevated CO_2 was attributed to higher rubisco activities but not attributed to more rubisco protein. Rubisco activities were regulated by CO_2 and by light flux density (Vu et al., 1986, 1987). For rice, rubisco activity expressed on a leaf area basis decreased by 66% across the 160 to 900 μmol mol^{-1} long term CO_2 treatments. A major cause of this decline in rubisco activity was a 32% decrease in the amount of rubisco protein relative to other protein (Rowland-Bamford et al., 1991). Specific soybean nodule activity was unchanged at elevated CO_2 (Philips et al., 1976; Finn and Brun, 1982), but total nodule dry matter was increased. Therefore, greater total nitrogen accumulation of plants at elevated CO_2 was attributed to more nodules rather than higher enzyme activities.

Temperature Effect and Its Interaction With CO_2

There have been many experiments conducted on the effects of temperature within the range of 15-30 °C (Thomas et al., 1978, 1981; Sionit et al., 1987a, 1987b; and Caulfield and Bunce, 1988). They found that higher temperature increased leaf photosynthesis, total dry matter production, leaf area index, seed number and seed yield. Only a few soybean experiments have been done with maximum daytime temperature above 30 °C. Baker et al. (1989) reported that as day/night temperature increased from 26/19 to 36/29 °C, total above ground dry matter and leaf area increased slightly. In that study, seed number increased with the increase in temperature but individual seed weight decreased, and seed yields were not significantly different. Campbell et al. (1990) reported that soybean canopy photosynthesis was very similar at temperatures ranging from 26 to 36 °C. No experiments have been conducted at daytime temperature higher than 36 °C for the entire growing season. The effects of high temperature on soybean growth throughout the growing season are still mostly unknown.

Temperature responses vary with crop species. Wolf et al. (1990) found that temperature up to 38 °C did not cause a reduction in the photosynthesis of potato (*Solanum tuberosum* L.) plants which had been grown at those temperature for a long period. Higher temperature (up to 40/42 °C), or the transfer of plants from daytime temperature regimes of 22 °C to 32 °C caused a reduction in net photosynthesis. They

concluded that a potato crop can be acclimated to grow and have an adequate rate of photosynthesis even at relatively high temperature. Source-sink relationships, which were modified by the later formation of tubers at higher temperatures did not affect photosynthesis.

Baker et al. (1992a, 1992b, 1993a, 1993b) reported the effects of high temperature ranges (day/night from 28/25 to 40/37 °C) on rice growth. Although the number of tillers and panicles increased at higher temperature, total above ground biomass and filled grain number decreased as temperature increased, and grain yield sharply decreased as day temperature increased from 34 to 40 °C. They concluded that potentially large negative effects on rice yield are possible if future air temperature rises. In warmer regions of the world, possible future increase in air temperature may result in yield decrease and increased water requirements. Rice grain yield declined by roughly 10% per each 1 °C rise in day/night temperature above 28/21 °C (Baker and Allen, 1993b). Reddy et al. (1991a, 1991b) reported cotton productivity responses to temperature at day/night temperature treatments of 21/10, 25/15, 30/20, 35/25 and 40/30 °C, respectively. They found the optimum temperature for photosynthesis was 35/25 °C; for dry matter accumulation, 30/20 °C; and for boll weight, 25/15 °C. Total dry matter and boll weight sharply decreased at temperatures of 35/25 and 40/30 °C. It is hypothesized that elevated temperatures have little effects on canopy

photosynthesis, but elevated temperature significantly reduces seed set percentage, filled grains and grain yields. Interactions between temperature and CO_2 have been reported. Based on simulation, Long (1991) proposed that an increase of CO_2 concentration from 350 to 650 μmol mol^{-1} can increase CO_2 uptake rate of wheat (in light-saturated condition) by 20% at 10 °C and 105% at 35 °C, and can raise the temperature optimum of CO_2 uptake by 5 °C. That is, elevated CO_2 may compensate for the negative effects of high temperature on photosynthesis by increasing CO_2 uptake (Boote and Pickering, 1994). There is an interaction between temperature and CO_2 on rice development. Manalo et al. (1994). reported that doubling CO_2 increased rice plant weight by 17% at day/night temperature 29/21 °C. Doubling CO_2 increased the days from sowing to flowering and flowering duration, but the effects varied with temperatures and species. On the other hand, Key et al. (1981) and Ougham et al. (1988) reported that plant thermotolerance was related to heat shock protein. One reasonable scenario is that reduced nitrogen content in elevated CO_2 condition might reduce the capacity of plants to adjust via heat shock protein. However, Coleman et al. (1991) reported that there was little relationship between plant nitrogen status and the ability of a plant to tolerate an acute increase in temperature.

There is also an interaction between temperature and CO_2 on respiration. Ziska and Bunce (1993) reported that growth respiration was reduced at 700 μmol mol^{-1} CO_2 and that

maintenance respiration decreased at doubled CO_2 only under low temperature (15/20 °C) for both grass and alfalfa.

Modeling Soybean Growth and Response to Environment

Many ecological factors such as solar energy, carbon dioxide, water, nutrients and biological aspects of the plants are involved in the crop production system. Those factors may directly or indirectly affect plant growth. Modeling the system can provide an indispensable method for system research for plant production.

The SOYGRO model (Jones et al., 1989) predicts soybean performance well under both existing climate and elevated CO_2 conditions. There are also other soybean growth models such as GLYCIM (Acock et al., 1983) and SOYMOD/OARDC (Meyer et al., 1979). SOYGRO is more user-friendly and has been much more widely validated and used than the other two models. The Decision Support System for Agrotechnology Transfer (DSSAT) includes the main field crops, uses standardized input and output, and provides operative information for decision making in system analysis of crop production (IBSNAT, 1989). Soybean growth models have been developed and modified from canopy level to leaf level and even biochemical processes (Boote et al., 1988, 1989; Boote and Loomis, 1991; Boote and Pickering, 1994).

Acock (1991) introduced an equation giving a hyperbolic dependence of net and gross photosynthetic rate (Pn and Pg)

respectively) on both the light flux density at the leaf surface (I) and CO_2 concentration (C):

$$Pn = \alpha I \tau C/(\alpha I + \tau C) - R$$

where α is leaf light-utilization efficiency (quantum efficiency), τ is leaf conductance to CO_2 transfer, and R is leaf dark respiration rate. By this equation, net photosynthesis increases with increasing CO_2 concentration and approaches the asymptote of αI . α is greater and τ is smaller for plants grown in elevated CO_2. The net photosynthesis increases linearly and then gradually becomes saturated as the internal CO_2 increases.

Temperature affects crop development and assimilation. Jones et al. (1991) described soybean development for individual phases by using photothermal coefficients and precisely predicted soybean development as a function of temperature and daylength.

Acock (1991) simply used two straight lines to describe the relationship between temperature and gross photosynthesis. Boote and Pickering (1994) developed equations to express the relationship between leaf photosynthesis and temperature and CO_2. Despite the linear increase in leaf electron transport rate with temperature, leaf photosynthesis and especially canopy assimilation becomes a nonlinear response to temperature and share a broad temperature optimum. The temperature and CO_2 responses predicted by this approach are very close to experimental data.

Curry et al. (1995) used soybean growth models to simulate soybean growth based on weather predicted by general circulation models. The results show a 60% increase in estimated water requirement for irrigation. The negative effects of climate change alone on soybean yields were mostly offset by the increased atmospheric CO_2 concentration for two scenarios of both irrigated and rainfed cases. Soybean production in the USA would not be adversely affected by climate change if the climate changes according to two of the general circulation models (GISS and GFDL), unless water supply for irrigation is limited. However, the UKMO scenario of climate change led to a prediction of decreased soybean yields (Curry et al., 1995). Soybean is apparently more tolerant to high temperature than other crops such as cotton and rice for which the elevated temperature caused severe adverse effects on reproductive growth. The positive yield response of cotton plants to high CO_2 declined sharply at higher temperatures, and abscission rate of fruiting structures increased rapidly (Reddy et al., 1995). For rice, modeling research show that yields will be decreased in warmer regions such as California and Southern China (Barry and Geng, 1995; Jin et al., 1995). On the basis of a series of rice experiments in Gainesville, Florida, Baker et al. (1995) summarized that in warmer areas of the world, possible future increases in air temperature may result in yield decreases and increased water requirements.

Rationale and Objectives

Atmospheric CO_2 concentration has been rising and climate is likely to change. Elevated CO_2 effects on crop photosynthesis and growth are generally positive; however, temperature increase has resulted in negative reported effects on the seed yields of some crop species. The interaction of temperature and CO_2 on soybean is relatively unknown, particularly at temperatures above 36 °C. Therefore, it is important to evaluate the effects of elevated temperature and doubled CO_2 on soybean growth and yield processes.

CHAPTER 2
EFFECTS OF ELEVATED TEMPERATURE AND CO_2 ON SOYBEAN PHOTOSYNTHETIC RATE

Introduction

Carbon dioxide and other greenhouse gases in the atmosphere have been increasing due to human activities. The atmospheric CO_2 concentration is projected to double and air temperature may increase by 1.5-4.5 °C in the next century (IPCC, 1990). Climate change may result in the reduction of crop and animal productivity and therefore may have important effects on agriculture.

Plant carbon exchange is directly coupled with CO_2 concentration in the atmosphere in which the plants are grown. Allen (1979), Kimball (1983), Cure and Acock (1986), and Allen (1990) reviewed plant responses to elevated CO_2. Leaf or canopy photosynthetic rate is greatly increased at elevated CO_2 concentration (Acock et al., 1985; Brun et al., 1967; Campbell et al., 1988; Egli et al., 1970; Havelka et al., 1984; Jones, et al., 1984a, 1985a, 1985b; Rogers et al., 1984; and Sionit et al., 1984, 1987). Doubled CO_2 increases total non-structural carbohydrate concentration (Allen et al., 1988; Baker et al., 1989, Vu et al., 1989). Soybean canopy CO_2 exchange rate was found to depend on the existing CO_2

concentration rather than CO_2 history to which the plants had previously been exposed (Jones et al., 1985a). On average, photosynthetic rates of C_3 plants are increased about 50% by a doubling of CO_2.

Caulfield and Bunce (1988) compared several soybean varieties and reported that the optimum temperature for soybean leaf photosynthetic rate was 25 °C in 350 μmol CO_2 mol^{-1} when compared in the temperature range from 18 to 30 °C. However, Campbell et al. (1990) reported that soybean canopy photosynthetic rate was similar across temperatures from 26 to 36 °C. Harley et al. (1985) studied the interactive effects of light, leaf temperature, CO_2 and O_2 on soybean photosynthetic rate. They reported that soybean leaf photosynthetic rate increased with photosynthetic photon-flux density, and that the optimum leaf temperature for light-saturated leaf photosynthetic rate at elevated CO_2 was around 35 °C.

Most previous experiments have focused on CO_2 effects only at ambient temperature. There have been few experimental studies of the interaction between elevated CO_2 and elevated temperature on soybean growth and photosynthetic rate, especially with temperatures higher than 35 °C. It is important to understand how doubled CO_2 and elevated temperature interactively affect carbon assimilation. The objective of this experiment was to study the effects of a range of elevated temperatures on soybean leaf and canopy photosynthetic rate at both ambient and doubled CO_2.

Materials and Methods

Controlled Environmental Chambers and Treatments

Eight outdoor sunlit, computer-managed, environment-controlled chambers were used for the experiment. The chambers consist of clear sixlight plastic (polyethylene terphthalate) tops and walls. The chamber dimensions were 1.0 m by 2.0 m in cross section by 1.5 m in height. These chambers transmit an average of 88% of the photosynthetic photon flux density. The photon flux above the chambers was measured continuously with a quantum sensor (LICOR Model LI-190SA, Lincoln, NE). Air was circulated through ductwork on the north side of each chamber by continuously operating circulation fans. Air dry bulb temperature, dew point temperature, and CO_2 concentration for each chamber were maintained with a dedicated sub-processor (Campbell CR10T) which operated in real time. Sensors were monitored at frequent (<10 s) intervals and the signals obtained were used in feedback algorithms to actuate various control devices. The Campbell CR10T was used to record air temperature, dew point and CO_2 concentration and manipulate the operations of temperature control, dew point control, and CO_2 injection. Carbon dioxide concentrations in each chamber were monitored by Siemens infrared gas analyzers and maintained by injecting CO_2 from high pressure cylinders. The amount of injected CO_2 was recorded, and the carbon exchange rate was calculated and

summarized every 5 minutes. Temperature in each chamber was controlled by using hot water and cold water coils in the system. N_2O, a leak test gas, was injected at 10:00 and 14:00 hours during the day and at hourly intervals at night. All data were downloaded periodically to a host PC processor. More details about the growth chamber system were described by Jones et al. (1984b) and Pickering et al. (1994).

Soil depth in the chambers was 60 cm. Plastic drainage pipe was set at the bottom of each chamber. The pipes were covered by a layer of gravel to the thickness of the pipe, followed by a 2-cm layer of coarse sand. Kendrick fine sand top soil was filled above the top of the sand layer. The drainage pipe was connected to a water source, and water was continuously supplied by a floating valve system to maintain the water table at 50 cm below the soil surface. The upward capillary flow of this fine sand soil provided an optimum water supply once the seedlings were more than 7-10 days old.

Temperature and CO_2 treatments for the experiments in 1993 and 1994 are summarized in Table 2-1. Because the treatment temperature in 1993 was not high enough to evaluate the full range of effects of elevated temperatures, data from 1994 experiment were mainly used for this study. Only a few plants at edge rows survived in the 48/38 °C treatment in 1994, thus this treatment was excluded from this report. The chamber air temperature and CO_2 concentration values averaged at 5-min intervals were used. The mean deviations between

Table 2-1. Growth chamber CO_2 and temperature treatments for soybean, cv. Bragg.

Temp.	CO_2			
	350		700	
°C	μmol mol^{-1}		μmol mol^{-1}	
48/38				S
44/34				S
40/30	F	S	F	S
36/26	F		F	S
32/22	F		F	S
28/18	F	S	F	S

F = Fall, 1993 S = spring, 1994

measured chamber air temperature, CO_2 concentration and their programmed values were about ±0.2 °C for temperature and around ±2.0 (maximum of 10) μmol mol^{-1} for CO_2 treatments. But short time deviation could be larger (Appendix 1, 2, 3, 4).

Plant Culture and Sampling

Soybean cultivar Bragg was grown from seeding to maturity in sunlit, controlled environment chambers at Gainesville, Florida. Seeds were inoculated with *Bradyrhizobium* just before planting. Soil in the chambers was Kendrick fine sand (loamy, siliceous, hyperthermic Arenic Paleudult) top soil. Magnesium sulfate was applied at the rate of 34 g m^{-2} and incorporated into the top 15 cm soil. To control rootknot nematodes, the soil was treated with Nemacur (Ethyl-3-methyl-4 phenyl phosphoramidate) at the rate of 4.48 g m^{-2} and mixed in the 15 cm top soil. Soybean seeds were sown on 19 August 1993 and 11 February 1994, respectively, in 32-cm rows. Plants were thinned to 75 plants m^{-2} at 11 days after planting (DAP).

Sampled plants were 9, 9, 6, 6, 6, 6, 6 and 6 plants m^{-2} at 18, 25, 32, 39, 46, 53, 71 and 85 DAP. Approximately 20 plants m^{-2} remained at final harvest time.

Measurement of Leaf Photosynthetic Rate

Leaf photosynthetic rate was measured with the LI-COR LI-6200, Steady State Photosynthesis System. The measurements were conducted at treatment conditions (the long term temperature and CO_2 environment) and at common 30 °C and 350 μmol mol^{-1} CO_2 (short time switching) conditions, respectively. Each leaf was measured for two consecutive 15-s intervals giving two mean values. The operator and LI-COR leaf cuvette were accessed through a trapdoor in the south side of each chamber. A special mask was used by the operator for breathing outside air so that CO_2 concentration in growth chamber remained well controlled. The first measurement was started when the temperature and CO_2 conditions in the growth chamber were stable at the programmed level. Temperature and CO_2 in the LICOR leaf cuvette were thus very close to those of the large growth chamber. Some parameters, such as leaf area and boundary layer conductance, were processed after the measurement. The data were downloaded to a computer.

Leakage Corrections Associated with Canopy Carbon Exchange

Chamber leakage for CO_2 was calculated on the basis of injected N_2O leakage. It is assumed that the dispersion rate

of CO_2 is the same as that of N_2O because the molecular weight of both N_2O and CO_2 is 44. The emission rate of N_2O from chamber soil was measured and it was too small to detect at μmol mol^{-1} unit level, therefore, N_2O emission from soil was ignored in the calculation of N_2O leakage. Computed CO_2 leakage is proportional to the CO_2 concentration difference between inside and outside of the chamber multiplied by a leakage coefficient computed from N_2O:

$CO_{2\ leakage} = K_{[N2O]} * ([CO_2]cham - [CO_2]amb)$ (μmol s^{-1} m^{-2})

Here $K_{[N2O]}$ is the leakage coefficient of N_2O, that is the amount (μmol) of N_2O leaked per second and square meter, per unit gradient of N_2O concentration under the chamber physical conditions, or $K_{[N2O]}$ =1/R, R = resistance coefficient.

$[CO_2]cham$ = CO_2 concentration in chamber (μmol mol^{-1})

$[CO_2]amb$ = CO_2 concentration in ambient air (μmol mol^{-1})

Leakage coefficient of N_2O was calculated according to:

PV = nRT, n=PV/RT

The μmoles of N_2O leaked, $\Delta n = (P_{[N2O]} * V/R*T) * 10^6$ (μmol) where Δn is the number of μmoles of N_2O leaked

$P_{[N2O]}$ is the change of N_2O partial pressure within time interval Δt

$= ([N_2O]_{t2} - [N_2O]_{t1}) * 10^{-6} * 1$ (atmosphere)

$[N_2O]_{t1}$: N_2O concentration in chamber at time t1 (μmol mol^{-1})

$[N_2O]_{t2}$: N_2O concentration in chamber at time t2 (μmol mol^{-1})

V: the chamber volume, 4185 liters

R: constant, 0.08205 (liter atmosphere mol^{-1} K^{-1})

T: temperature in the chamber, °K

$K_{[N2O]}$ is calculated as:

$$K_{[N2O]} = \{([N_2O]_{t2} - [N_2O]_{t1}) * V/R*T\}/\{([N_2O]cham - [N_2O]amb) * \Delta t * AREA\}$$

where $[N_2O]cham$: N_2O concentration in chamber (μmol mol^{-1})

$[N_2O]amb$: ambient N_2O concentration (μmol mol^{-1}), assumed zero.

Δt = t2-t1 in seconds

AREA = Chamber land area in square meters (2 m^2)

$$K_{[N2O]} = \{([N_2O]_{t2} - [N_2O]_{t1}) * V/R*T\}/\{([N_2O]cham) * \Delta t * AREA\}$$

Average $[N_2O]$ in the chamber at that instant is:

$$[N_2O]cham = ([N_2O]_{t2} + [N_2O]_{t1})/2$$

Finally, the leakage coefficient is calculated as:

$$K_{[N2O]} = \{([N_2O]_{t2} - [N_2O]_{t1}) * V/R*T\}/\{0.5*([N_2O]_{t2} + [N_2O]_{t1}) * \Delta t * AREA\}$$

Calculation of Respiration and Canopy Gross Photosynthetic Rate

Night time carbon exchange rate (NCER) equals recorded carbon exchange rate (RCER, defined as negative values for respiration) minus leaked CO_2 (leakage out is defined as positive value), NCER = RCER-leakage. Soil respiration should be included in NCER for the calculation of gross photosynthesis. Apparent daytime carbon exchange Rate (DCER) can be expressed as recorded daytime carbon exchange rate (defined as positive values for photosynthetic rate) minus daytime leakage, DCER = RCER-leakage.

To have an accurate estimation of total photosynthetic CO_2 uptake, daytime respiration should be included. The computer system maintains the CO_2 concentration in the chamber by injecting CO_2. When plant respiration (and soil CO_2 efflux) releases CO_2 into the chamber, the system will inject less CO_2 to maintain CO_2 level in the chamber. Gross photosynthetic rate will thus be underestimated if the calculation is based on computer-recorded CO_2 injections only. Linear relationships between the night time respiration (NCER) and chamber temperature (Tn) were derived from hourly NCER and its Tn variation for each chamber (NCER = k*Tn + b). The relationship between daytime respiration and chamber air temperature was assumed to be the same as that at night for the same 24-hour period. Projected daytime respiration (Rd, negative values) were calculated with coefficients (k, b) obtained from night time respiration but using the daytime chamber air temperature (Td) for each chamber (Rd = k*Td + b). Canopy gross photosynthetic rate (Pg) was computed as the sum of daytime carbon exchange rate (positive values) and daytime respiration Pg = DCER - Rd.

A special study was conducted to evaluate the procedure for estimation of daytime respiration. At midday of 36 and 60 DAP in 1994, each chamber was completely covered with a large sheet of black plastic for 45 minutes to create zero photosynthetically active radiation in the chambers. Daytime respiration (including soil respiration) was then measured.

Table 2-2 shows that there was no significant difference between measured daytime respiration and estimated respiration Rd, thus confirming the validity of the respiration approach to estimate daytime Rd and Pg.

Table 2-2. Estimated and measured (12:00-13:00 hours) respiration rates# at treatment condition at 36 DAP, and at a common 30 °C at 60 DAP.

Treatments °C-(μmol mol^{-1})	DAP 36		DAP 60	
	Obs.	Pred.	Obs.	Pred.
	--------μmol CO_2 m^{-2} s^{-1}----------			
44/34-700	12.9	12.5	10.7	11.2
40/30-700	12.3	11.8	11.0	10.6
36/26-700	13.0	13.5	12.4	12.0
32/22-700	8.0	9.4	12.4	11.9
28/18-700	7.6	9.6	14.1	12.7
40/30-350	8.5	9.1	9.7	8.0
28/18-350	5.5	6.4	10.2	8.4
t-Test	----- NS ----		----- NS ----	

corrected with soil respiration, NS: non-significant

Statistical Analysis

The General Linear Model (GLM) and T-test Procedures as described in the SAS User's Guide Statistics (SAS Institute, Inc. 1987) were used for the analyses.

Results and Discussion

Leaf Photosynthetic Rate

Leaf apparent photosynthetic rate of the plants grown at doubled CO_2 was significantly affected by growth temperature (Figure 2-1). At 700 μmol CO_2 mol^{-1}, the optimum air temperature for leaf photosynthetic rate was the 40/30 °C

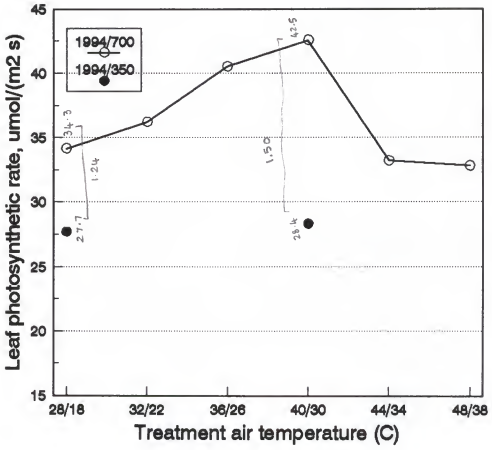


Figure 2-1. Soybean leaf photosynthetic rate measured under long-term treatment conditions at 46 DAP in 1994. Statistical tests on temperature (quadratic) effect and CO_2 effect were significant at 0.01 level.

treatment whereas leaf photosynthetic rate at 350 μmol CO_2 mol^{-1} was no higher at 40/30 °C than 28/18 °C. This supports the hypothesis that the optimum temperature for photosynthetic rate is higher under elevated CO_2 conditions based on simulation results of Long (1991), and Boote and Pickering (1994). The optimum of 40/30 °C air temperature is consistent with the measurements of Harley et al. (1985) who reported that leaf photosynthetic rate at elevated CO_2 was the highest at leaf temperature of 35 °C. The difference between air temperature and leaf temperature for the 40/30 °C treatment was 4-5 °C in midday, thus the leaf temperature was about 35 °C during midday measurement of this treatment. There was a significant difference in photosynthetic rate between ambient CO_2 and doubled CO_2 treatments at the same temperature conditions. Elevated CO_2 increased leaf photosynthetic rate by 25% at 28/18 °C and 50% at 40/30 °C when measured under treatment condition. In 48/38 °C treatment, the only plants that survived the seeding stage were located at the east and west rows where the maximum air temperature was around 45 °C because of the heat transfer through the sixlight walls. This is one reason that leaf photosynthetic rate of both 48/38 and 44/34 °C was very close. Apparently, growth processes are more sensitive to temperature than photosynthetic processes.

Measurements made at a common 30 °C and 350 μmol CO_2 mol^{-1} showed that leaf photosynthetic rate was significantly influenced by the treatment temperature under which the plants

had previously grown (Figure 2-2). These data indicate that leaves grown in a long term temperature environment have different photosynthetic characteristics. In this case, the optimum growth temperature for photosynthetic rate was lower, 36/26 °C rather than 40/30 °C, and the highest temperature treatment leaves had the lowest photosynthetic rate at 30 °C, suggesting slight long-term heat stress resulting from the two highest temperature treatments. The plants previously grown at 700 μmol mol^{-1} CO_2 had average 10% lower leaf photosynthetic rates than those previously grown at 350 μmol mol^{-1} long term CO_2 treatment, which suggests that there was small downward photosynthetic acclimation to elevated CO_2. In this experiment, the leaves which had been grown at ambient CO_2 were a little greener than those grown at doubled CO_2. This color difference might indicate a lower protein or nitrogen concentration in the doubled CO_2 leaves than in the ambient CO_2 treatments.

Canopy Gross Photosynthetic Rate

Diurnal response

At 35 DAP, canopy gross photosynthetic rate was the highest at 36/26 °C (Figure 2-3). At this vegetative growth phase, treatment temperatures higher or lower than 36/26 °C decreased canopy gross photosynthetic rate although the 40/30 °C treatment was nearly the same as the 36/26 °C treatment. These results are very similar to the response of cotton

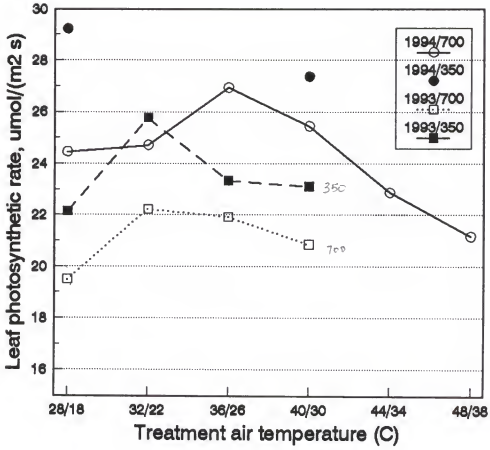


Figure 2-2. Effect of long-term temperature history on soybean leaf photosynthetic rate measured at 30 °C and ambient CO_2 concentration at 53 DAP in 1994, 32, 41 and 54 DAP in 1993. Statistical tests on temperature (quadratic) effect and CO_2 effect in 1994 were significant at 0.05 level. The t-Test for two history group in 1993 was significant at 0.05 level.

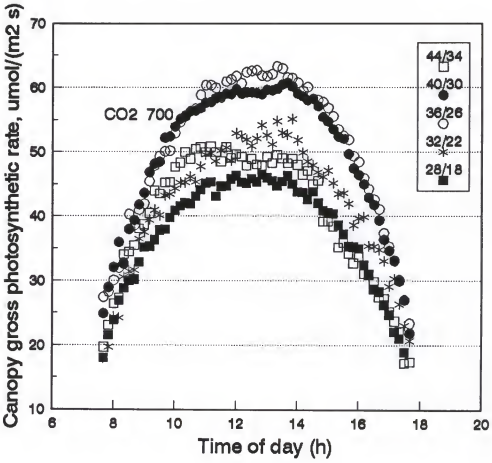


Figure 2-3. Effect of temperature on diurnal changes in soybean canopy gross photosynthetic rate at 35 days after planting in 1994.

plants (Reddy et al., 1991). Diurnal temperature was programmed to be maximum at 15:00 hours. Canopy gross photosynthetic rate of the 44/34 °C treatment began to decrease at 11:30, earlier than other treatments, with a sharp decrease after 14:00 hours. This indicates that air temperature approaching 44 °C temperature began to inhibit canopy gross photosynthetic rate, possibly causing stomata closure or partial enzyme inactivation. The difference of canopy gross photosynthetic rate among the treatments at 35 DAP is also related to leaf area index resulting from long-term temperature treatments. In this case, canopy gross photosynthetic rate increased for a larger leaf area index canopy. Doubling CO_2 increased canopy gross photosynthetic rate about 50% for both 28/18 and 40/30 °C treatment (Figure 2-4). The increase of gross photosynthetic rate was due to the direct effect of doubled CO_2 and larger leaf area index caused by long term CO_2 exposure. The analysis of the gross photosynthetic rate mean values obtained from 11:00 to 14:00 hours showed that the effect of temperature (quadratic) and CO_2 on canopy gross photosynthetic rate was statistically significant at $P \leq 0.01$ level, and the optimum daytime temperature was around 35 °C (Figure 2-5).

Response to PAR

Canopy photosynthetic rate responded almost linearly to photosynthetic active radiation (PAR) at 35 DAP especially over the range 500-1700 μmol photon m^{-2} s^{-1} (Figure 2-6).

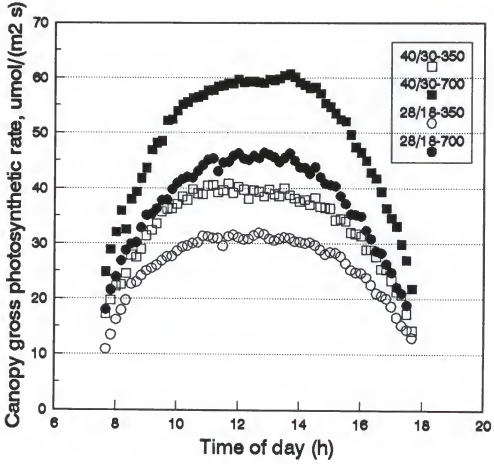


Figure 2-4. Effect of CO_2 on diurnal changes in soybean canopy gross photosynthetic rate at 35 days after planting in 1994.

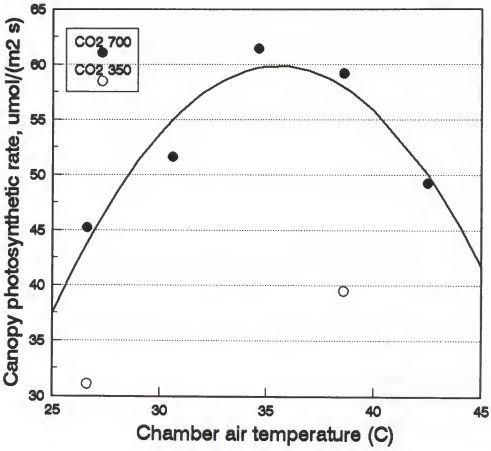


Figure 2-5. Effects of long-term chamber air temperature and CO_2 concentration on soybean canopy gross photosynthetic rate measured from 11:00 to 14:00 hours at 35 days after planting in 1994. Statistical tests on temperature (quadratic) effect and CO_2 effect were significant at 0.01 level.

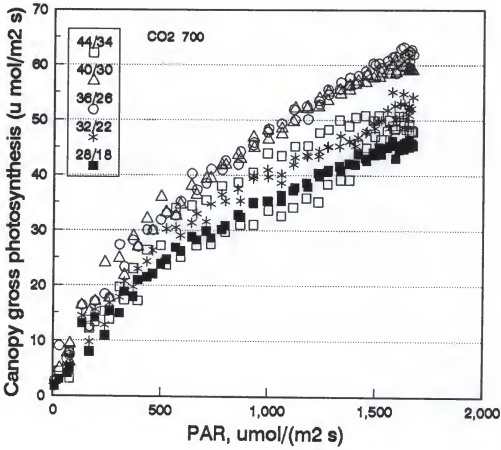


Figure 2-6. Effect of temperature on soybean canopy gross photosynthetic rate response to photosynthetic active radiation (PAR) at 35 days after planting in 1994.

Canopy photosynthetic rates did not approach light-saturation even as PAR increased to 1700 μmol m^{-2} s^{-1}. Canopy gross photosynthetic rate of the 44/34 °C treatment in the afternoon was much lower than that in the morning under the same PAR condition. This was due to heat stress at noon (temperatures of 40 to 44 °C) as mentioned before. Doubled CO_2 treatments increased canopy gross photosynthetic rate responses to PAR (Figure 2-7). There was a difference in light responses between morning and afternoon. It was mainly caused by different chamber air temperatures or might be carbohydrate loading limitation at the same PAR level.

Acclimation to CO_2

Short term CO_2 switching treatments were made to determine the canopy photosynthetic acclimation to CO_2 and temperatures (Figure 2-8). The results showed that canopy photosynthetic rate increased with increasing CO_2 for different temperature history treatments. Under the same CO_2 concentration, temperature affected canopy gross photosynthetic rate by indirect effects via greater leaf area index caused by higher long-term temperature treatment. For different CO_2 history treatments (Figure 2-9), there was no difference in canopy gross photosynthetic rate for 40/30 °C treatments but there was a difference for 28/18 °C treatments. Effects were attributed to difference of leaf area index of only 2% for 40/30 °C treatment and 19% for 28/18 °C treatment. Leaf area index can play a key factor in different canopy

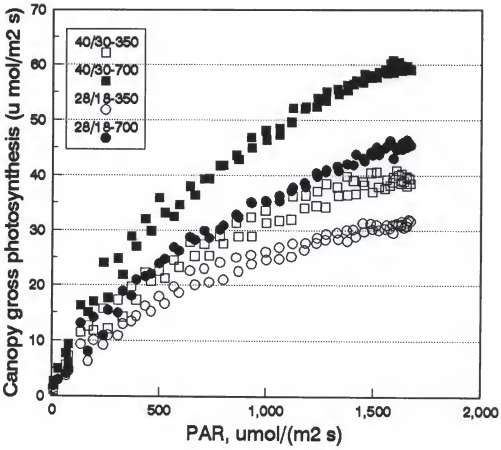


Figure 2-7. Effect of CO_2 on soybean canopy gross photosynthetic rate response to photosynthetic active radiation (PAR) at 35 days after planting in 1994.

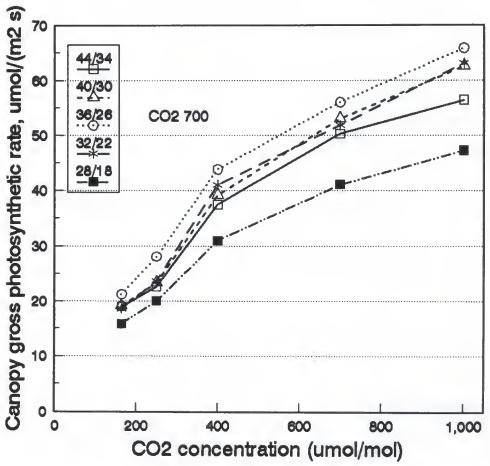


Figure 2-8. Soybean canopy gross photosynthetic rate responses to a range of short-term imposed CO_2 concentrations as affected by temperature treatment history for plants grown at 700 μmol mol^{-1} CO_2 at 31 days after planting in 1994.

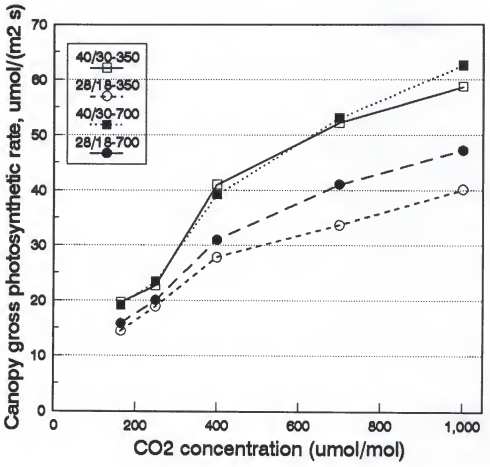


Figure 2-9. Soybean canopy gross photosynthetic rate responses to a range of short-term imposed CO_2 concentrations as affected by CO_2 and temperature treatment history at 31 days after planting in 1994.

gross photosynthetic rates. Jones et al. (1985a) also reported that, at ambient CO_2 condition, carbon exchange rate of the plants grown at long term doubled CO_2 was higher than that of the plants grown at ambient CO_2. The apparent upward acclimation of canopy photosynthetic rate was thereby primarily due to the higher leaf area index in this case.

Acclimation to temperature

To evaluate instantaneous response versus temperature acclimation, all chamber temperatures were initially set at the same high value and then gradually cooled from 42 to 26 °C which was nearly the mean temperature of the lowest temperature treatment at 59 DAP. Gross photosynthetic rate of the 44/34 °C treatment decreased when temperature was cooled from 42 to 26 °C (Figure 2-10). Canopy photosynthetic rate of other treatments increased as the temperature cooled down, the increasing rate of canopy gross photosynthetic rate was the largest for the lowest long term temperature treatment. Plants which had different long-term CO_2 history but same temperature history had similar increasing rate of canopy gross photosynthetic rate when instantaneous temperature was decreased from 42 to 26 °C (Figure 2-11). This indicates that the optimum temperature for canopy photosynthetic rate varied with long term temperature treatments. It seems that the closer the instantaneous temperature to the long term temperature, the higher the canopy photosynthetic rate. These results indicate that plants could acclimate to long term

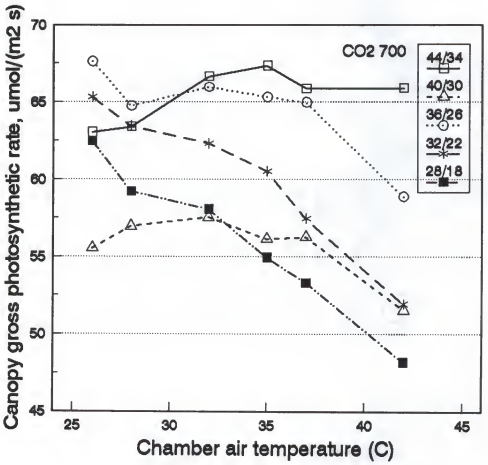


Figure 2-10. Effect of temperature history on soybean canopy gross photosynthetic rate response to short-term temperature changes at 59 days after planting in 1994. The temperature switching started at 11:00 am at high temperature and ended at 12:00 noon at low temperature.

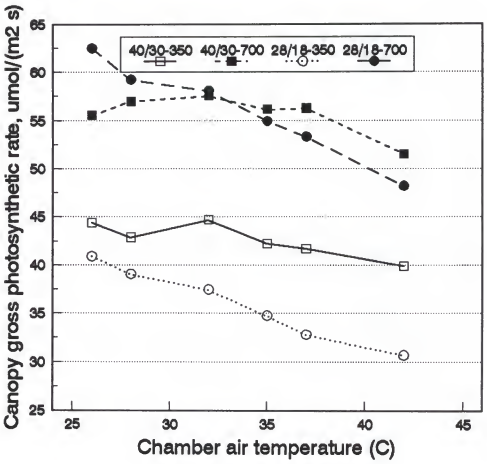


Figure 2-11. Effect of CO_2 history on soybean canopy gross photosynthetic rate response to short-term temperature changes at 59 days after planting in 1994. The temperature switching started at 11:00 am at high temperature and ended at 12:00 noon at low temperature.

temperature environment. These results indicate that the increase in temperature optimum for leaf and canopy photosynthetic rate might be caused not only by doubled CO_2 (Long, 1991) but also by elevated temperature. Wolf et al. (1990) found that temperature up to 38 °C did not cause a reduction in the photosynthetic rate of potato plants which had been grown at those temperatures for long periods prior to measurement. High temperature of 40/42 °C, or the transfer of potato plants from daytime temperature regimes of 22 °C to 32 °C caused a reduction in net photosynthetic rate. The potato plant responses also showed temperature acclimation. However, the mechanism of soybean thermal acclimation needs further study to explain the process.

Seasonal responses

Daily total gross photosynthetic rate (DTGP) varied gradually during the season with the change in leaf area index, whereas the sharper day-to-day variation was associated with PAR variation (Figure 2-12, 13, 14). Elevated CO_2 significantly increased DTGP for both 40/30 and 28/18 °C treatments (Figure 2-13, 14). DTGP increased rapidly in the first 30 days as the leaf area increased exponentially (Figure 2-15, 16), then stayed high about 40 days, and finally declined gradually. DTGP of the coolest temperature (28/18 °C) treatment was the slowest to increase during the first 30 days because leaf area grew more slowly. DTGP of the highest temperature (44/34 °C) declined the slowest during seed

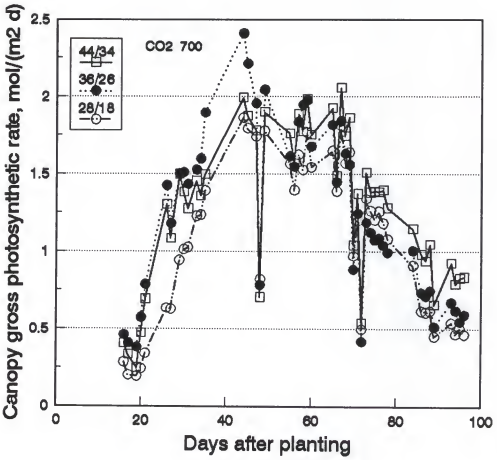


Figure 2-12. Effects of temperature on seasonal changes of the daily total soybean canopy gross photosynthesis in 1994. Test (GLM) of temperature effect was significant at 0.01 level.

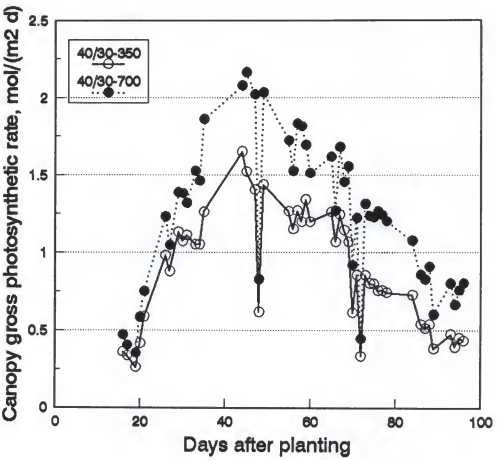


Figure 2-13. Effect of CO_2 on seasonal changes of the daily total canopy gross photosynthesis for soybean grown at 40/30 °C in 1994. Test (GLM) of CO_2 effect was significant at 0.01 level.

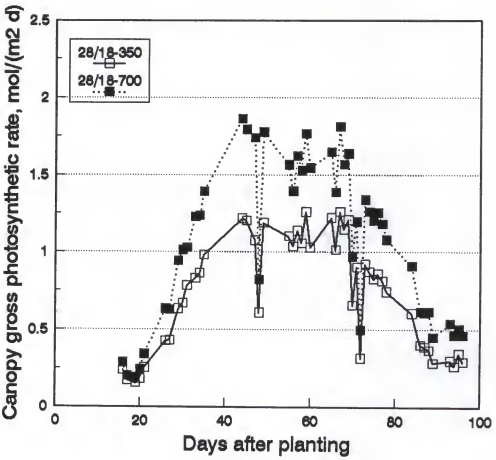


Figure 2-14. Effect of CO_2 on seasonal changes of the daily total canopy gross photosynthesis for soybean grown at 28/18 °C in 1994. Test (GLM) of CO_2 effect was significant at 0.01 level.

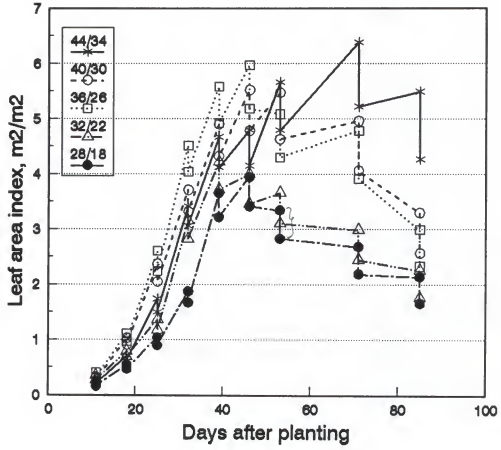


Figure 2-15. Seasonal leaf area index as affected by treatment temperatures at doubled CO_2 in 1994.

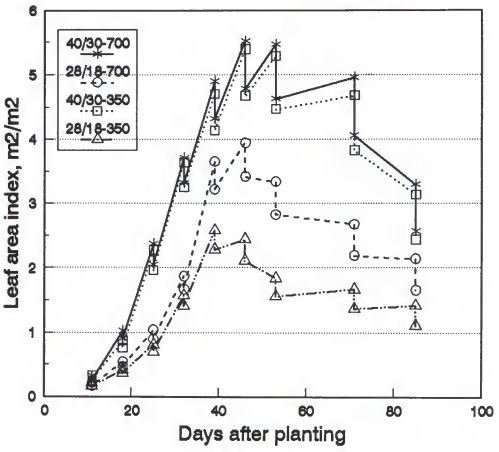


Figure 2-16. Seasonal leaf area index as affected by treatment temperatures and doubled CO_2 in 1994.

development and filling phase because development was prolonged by high temperature. The DTGP of the 44/34 °C treatment was the highest during the reproductive phase presumably due to a smaller sink size (fewer pods and seeds). On the other hand, these plants acclimated to the long term high temperature and the canopy gross photosynthetic rate remained high. It might be concluded that doubled CO_2 and elevated temperature (1.5 to 4.5 °C higher) will not cause a lower carbohydrate supply from photosynthetic rate in soybean.

Summary

Leaf photosynthetic rate at 700 μmol CO_2 mol^{-1} increased with increasing treatment temperature from 28/18 to 40/30 °C, then decreased as temperature increased further. Doubled CO_2 significantly increased both leaf and canopy photosynthetic rate. The 36/26 °C, 700 μmol CO_2 mol^{-1} treatment had the highest canopy gross photosynthetic rate during vegetative growth. Canopy photosynthetic rate of the 44/34 °C, 700 μmol CO_2 mol^{-1} treatment was the highest during reproductive growth, because it had the largest leaf area index. However, soybean under this treatment partitioned very little photoassimilate to the seeds. The optimum temperature for photosynthetic rate was increased by both doubled CO_2 and plant acclimation to high temperature. These results indicate that anticipated temperature increase under doubled CO_2 will not significantly affect canopy photosynthetic rate. Elevated temperature (1.5

to 4.5 °C higher) is not expected to cause carbohydrate source limitation in soybean.

CHAPTER 3
EFFECT OF ELEVATED TEMPERATURE AND DOUBLED CO_2 ON DARK RESPIRATION

Introduction

Carbon dioxide concentration in the atmosphere has been continuously increasing because of industrialization of the world. It is expected that present CO_2 concentration will double during the next century, and also that air temperature will increase because of the increase in greenhouse gases in the atmosphere (IPCC, 1990 and 1992). Elevated CO_2 generally increases plant photosynthesis, total dry matter and seed yields (Allen, 1979; Kimball, 1983; Cure and Acock, 1986; Allen 1990). Both elevated CO_2 and elevated temperature may have direct or indirect effects on plant respiration metabolism (Amthor, 1991). Gifford et al. (1985) found that growth of wheat (*Triticum aestivum* L.) in high atmospheric CO_2 was associated with up to 45% reduction in respiration by both root and whole plants. In their study, elevated CO_2 did not decrease the respiration for Mung bean (*Vigna radiata* L.) and sunflower (*Helianthus annuus* L.) plants. Baker et al. (1992c) reported whole canopy specific respiration decreased with increasing CO_2 across the range of 160 to 500 μmol mol^{-1}. Specific respiration rate of rice was associated directly with

nitrogen concentration of the plants. Also in that study, maintenance respiration was almost the same at both ambient and doubled CO_2.

There is an interaction between CO_2 and temperature on dark respiration. Ziska and Bunce (1993) reported that elevated CO_2 decreased maintenance respiration at 15/25 °C but increased it at 30 °C, while elevated CO_2 also decreased growth respiration at 20/30 °C for alfalfa (*Medicage sativa* L.) in comparison with ambient CO_2. Direct effects of CO_2 on leaf respiration have varied with treatment temperature (Ziska and Bunce, 1994a). Thomas and Griffin (1994) found that the maintenance coefficient of respiration was increased 34% by 710 μmol CO_2 mol^{-1} which was attributed to a 33% increase in leaf total nonstructural carbohydrate concentration of soybean [*Glycine max* (L.) Merr.] plants. By contrast, the growth coefficient was not significantly affected by CO_2 concentration.

For the analysis of maintenance and growth respiration, different methods have been developed. McCree (1970) and Hesketh (1971) used the regression method which is based on the relationship among respiration, photosynthesis and dry matter accumulation. The starvation method was used by McCree and Silsbury (1978) to estimate the minimal maintenance requirement. The mature tissue method (Wilson, 1975) is somewhat similar to starvation method. Based on biochemical knowledge, Penning de Vries (1975) provided a rather

sophisticated theoretical estimation method. Each method has its own advantages and disadvantages. In this study, a well-controlled chamber system made it possible to measure photosynthetic carbon exchange rate and dark respiration continuously at 5-min intervals (Jones et al., 1984b). The growth data were also available. The regression method was therefore chosen to analyze the growth and maintenance respiration. The objective of this study was to evaluate the direct and indirect effects of CO_2 and temperature and the interaction between CO_2 and temperature on dark respiration.

Materials and Methods

The experiments were conducted at the Irrigation Research and Education Park, University of Florida in Gainesville. Soybean [*Glycine max* (L.) Merr.] plants were grown season-long in eight sunlit, controlled-environment growth chambers. The experimental treatments, plant culture and controlled-environment chambers for studies conducted in 1993 and 1994 were described in chapter 2. Day and night CO_2 exchange rate was adjusted for leakage as described in Chapter 2.

Calculation of Dark Respiration

Each chamber was vented hourly at night and CO_2 concentration returned to near ambient level shortly after venting. Night time CO_2 exchange rate (CER) was calculated from the rate of increase of CO_2 released from plants in each

chamber. Whole canopy dark respiration (Rd) rates were calculated as CER adjusted for leakage, then subtracting soil respiration (Rs):

Rd = CER + Leakage -Rs

To evaluate the temperature effect on respiration, night-time chamber air temperatures were set at constant values (equal to the mean treatment temperature) during the night of 32 DAP. A similar study was conducted with temperature set at 30 °C for all chambers during the night of 60 DAP. Statistical tests showed that when temperature was constant there was no significant difference between the mean values of dark respiration measured between 21:00 to 22:00 hours and that measured between 4:00 to 5:00 hours (Table 3-1). Therefore, respiration did not change with time during the dark period because of possible shortage of carbohydrate, regardless of ambient or doubled-ambient CO_2 growth conditions. The estimation of soil respiration was based on the measurement of CO_2 released from the soil on the day before seed germination. It was assumed that soil respiration rate was the same during the growing season. Soil respiration was measured at the day before planting. It was estimated from 1.5 to 3.0 μmol CO_2 m^{-2} s^{-1} from the lowest to highest temperature treatments.

Leaf and Stem Nitrogen Concentration Analysis

Nitrogen analysis was done by weighing a 100 mg sample in a 100 ml test tube, adding 3.2 g salt-catalyst mixture

Table 3-1. Comparison of night time dark respiration rates# of soybean canopies measured at 21-22 h and 4-5 h at indicated fixed temperature from two nights in 1994.

Treatment	DAP 32-33			DAP 60-61		
Temp.-CO_2 °C-μmol mol^{-1}	Temp. °C	Mean Resp. μmol CO_2 m^{-2} s^{-1}		Temp. °C	Mean Resp. μmol CO_2 m^{-2} s^{-1}	
		21-22h	4-5h		21-22h	4-5h
44/34-700	37	7.34	6.10	30	10.89	10.82
40/30-700	33	7.67	7.66	30	10.59	10.24
36/26-700	29	7.74	7.67	30	11.84	11.89
32/22-700	25	5.64	5.76	30	11.69	11.46
28/18-700	21	5.01	4.73	30	12.34	12.27
40/30-350	34	5.34	5.60	30	7.81	7.43
28/18-350	21	3.28	2.70	30	7.99	7.96
t-Test		NS			NS	

corrected with soil respiration, NS: not significant

(anhydrous K_2SO_4-anhydrous $CuSO_4$, in a 9:1 ratio), 10 ml concentrated H_2SO_4, and mixing on a vortex mixer. Two glass boiling beads were added and the samples were then digested at 370 °C on an aluminum digestion block for 4 h (Gallaher et al., 1975), brought to 75 ml volume, transferred to Nalgene storage bottles, and analyzed with an Auto-analyzer (Agronomy Lab, UF).

Calculation of Maintenance Respiration and Synthesis Efficiency

Data from 43 to 49 days after planting (DAP) in 1994 were used for analysis. The calculation was done with the following equation from Fernandez (1977) and Stahl and McCree (1988):

Net gain = Yg * (gross input - m * biomass) [1]

Daily net gain (g CO_2 m^{-2} d^{-1}) or carbon accumulation rate was calculated as the difference between D (the sum of day-time

apparent photosynthesis and total soil respiration, g CO_2 m^{-2} d^{-1}) and N (the sum of total night time carbon exchange minus total night time soil respiration, g CO_2 m^{-2} d^{-1}). (Irving and Silsbury, 1987). Yg is the carbon synthesis efficiency (g CO_2 g CO_2^{-1}). Gross input (P) was estimated as sum of total apparent canopy photosynthesis (corrected for leakage) and total day-time respiration including soil respiration and plant respiration (g CO_2 m^{-2} d^{-1}), and m is maintenance respiration coefficient (g CO_2 g CO_2^{-1} d^{-1}). Biomass (g CO_2 m^{-2}) was calculated as: Biomass=M*S*V*(44/12). Here M is the sampled dry weight (g $plant^{-1}$), root biomass was estimated as 10% to 17% of the dry matter above ground from highest to lowest temperature treatment on the basis of the relationship between the temperature and root biomass at harvest time. The S is the number of plants (plant m^{-2}) in each chamber. The V is the coefficient to convert dry matter to carbon (g carbon g^{-1} dry matter). The carbon content of structural carbohydrates is on average 0.4504 g g^{-1} (Penning de Vries, 1982), and 44/12 is used to convert carbon to CO_2. The equation then can be expressed as:

$$D\text{-}N = Yg * P + b \qquad [2]$$

The available data were D, N and P. Linear regression between D-N and P was computed, and the slope Yg and constant b were therefore obtained. Since b=m*biomass*Yg (equation [1] and [2]), the maintenance respiration coefficient was calculated as m=b/(Yg*biomass).

Statistical Analysis

All statistical analyses, such as General Linear Model and t-Text, were conducted using SAS procedures described in the SAS user's manual (SAS Institute, Inc., 1987).

Results and Discussion

Whole Plant Respiration

Within each treatment, whole plant respiration increased with temperature (Figure 3-1). Among the different temperature treatments, the 36/26 °C and 700 μmol CO_2 mol^{-1} treatment had the highest respiration rates. Respiration rates were less when growth temperature was higher or lower than 36/26 °C. This was due to the difference of gross photosynthate produced each day, the accumulated dry matter and current chamber temperature. Plants grown at 36/26 °C had the highest canopy photosynthetic rate, highest leaf area index, and greatest dry matter at 35 DAP. Plants grown at doubled CO_2 concentration had significantly higher canopy respiration rates than those grown at ambient CO_2 (Figure 3-2), because they had larger photosynthetic rates and dry matter accumulation.

Seasonal Changes in Whole Plant Dark Respiration

Seasonally, whole plant night time respiration of soybean (Figure 3-3) increased rapidly until 40 DAP and remained high for about 30 days in the middle of growing season, then

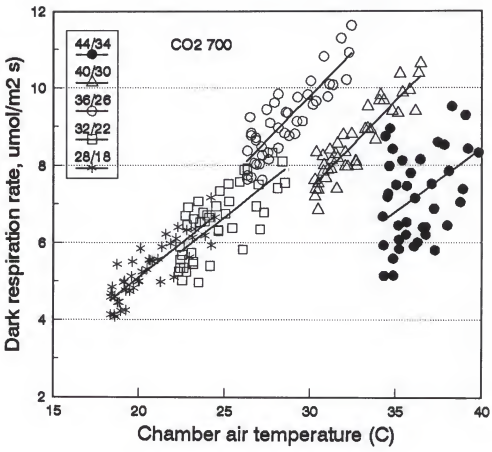


Figure 3-1. The effect of measurement temperature and five growth temperature treatments on whole plant dark respiration rates of soybean from 20:00 h at 35 DAP to 5:30 h at 36 DAP in 1994.

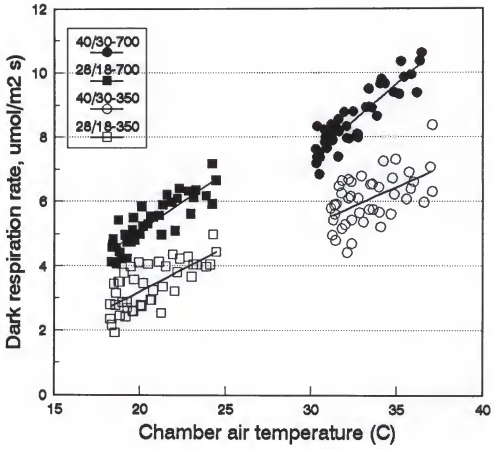


Figure 3-2. The effect of growth temperature and CO_2 treatments on whole plant dark respiration rates of soybean from 20:00 h at 35 DAP to 5:30 h at 36 DAP in 1994.

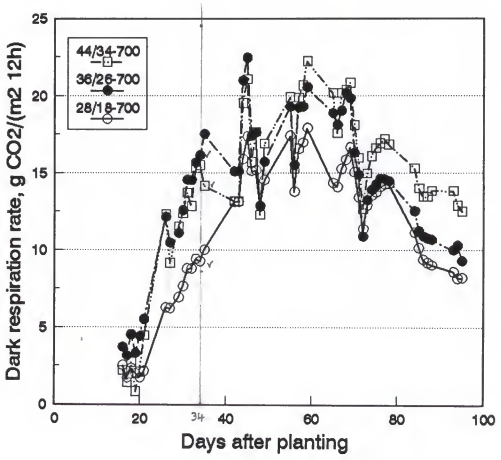


Figure 3-3. The effect of growth temperature on seasonal whole plant dark respiration of soybean in 1994.

decreased slowly as the plants senesced. Seasonal variation in whole plant respiration was mainly due to the seasonal time course of daily gross photosynthesis (Figure 2-13, 2-14, 2-15) and accumulation of dry matter (Figure 5-10). Plants grown in 28/18 °C and 700 μmol CO_2 mol^{-1} had a longer lag in dark respiration for the first 40 days because of the slower canopy expansion and slower development of the photosynthetic capacity at this lower temperature treatment. Plants grown at 36/26 °C had the highest dark respiration because this treatment had the optimum temperature for photosynthesis and vegetative growth. After 70 DAP dark respiration of the 44/34 °C treatment was the largest. This is because the 44/34 °C temperature treatment had the slowest reproductive development and the highest leaf area index, both caused by the high temperature.

Soybean plants grown at 700 μmol CO_2 mol^{-1} had 35-40% greater dark respiration in comparison with those grown at 350 μmol CO_2 mol^{-1} (Figure 3-4 and 3-5). This was attributed to higher photosynthesis rate and higher dry matter. It is clear that the plants grown at both elevated temperature and elevated CO_2 had increased dark respiration. However, higher respiration does not necessarily mean less dry matter accumulation, because doubled CO_2 increased photosynthesis 50% in comparison with ambient CO_2. Elevated temperature had little effect on photosynthetic rate as described in Chapter 2 but increased leaf area could possibly compensate for part

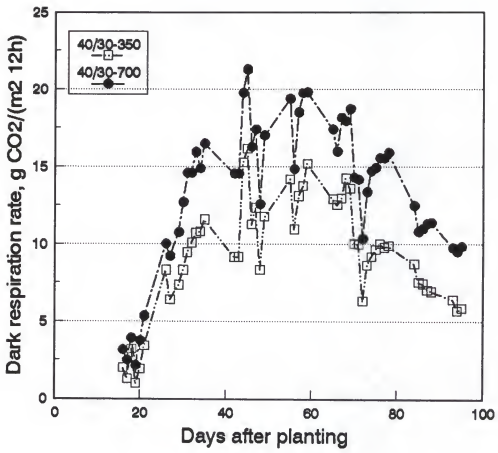


Figure 3-4. The effect of CO_2 levels on seasonal whole plant dark respiration of soybean grown at 40/30 °C in 1994.

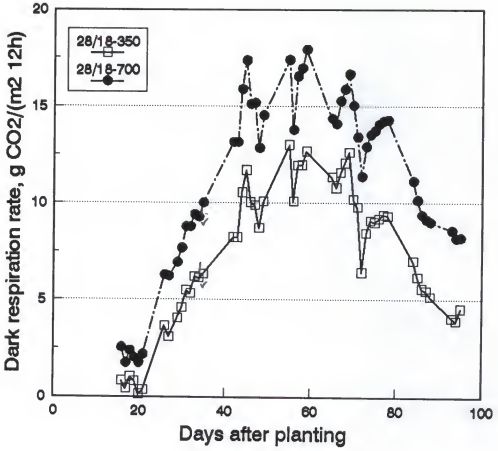


Figure 3-5. The effect of CO_2 on seasonal whole plant dark respiration of soybean grown at 28/18 °C in 1994.

of added carbon loss from dark respiration caused by elevated temperature. Therefore, elevated temperature had little effect on dry matter accumulation.

Daily and Seasonal Specific Respiration

Seasonal whole plant specific respiration (g CO_2/g dry matter) of soybean decreased with increasing development stage. Before 40 DAP, specific respiration decreased as the treatment temperature decreased (Figure 3-6). But after 40 DAP, the specific respiration of the 36/26 °C treatment became the lowest and that of 32/22 °C treatment the second lowest. Specific respiration appeared to be mainly determined by the development stage of the plants and secondarily by temperature. The low specific respiration of the 36/26 °C treatment after 40 DAP may be related to development stage because the growth and development for 36/26 °C treatment was among the fastest of the treatments. Specific respiration of plants grown at elevated CO_2 was higher at 40/30 °C, but lower at 28/18 °C in comparison with that at ambient CO_2 (Figure 3-7 and 3-8). Doubled CO_2 increased carbohydrate production which increased substrate for respiration in both temperature treatments. At 40 °C, temperature was high enough to allow higher dark respiration of these substrates. However, at 28/18 °C respiration was limited at low temperature and possibly was not able to use as much substrate. The extra substrate produced by elevated CO_2 at low temperature would be

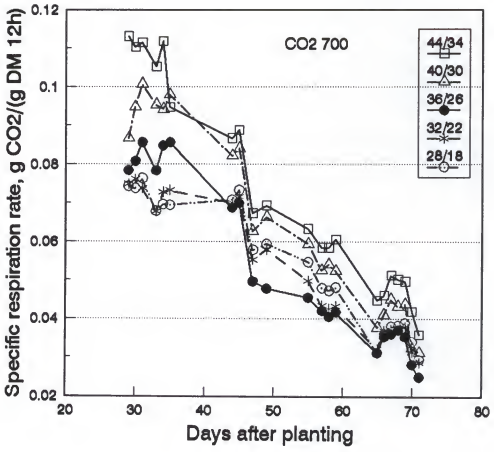


Figure 3-6. The effects of growth temperature on seasonal trend in whole plant specific dark respiration of soybean in 1994.

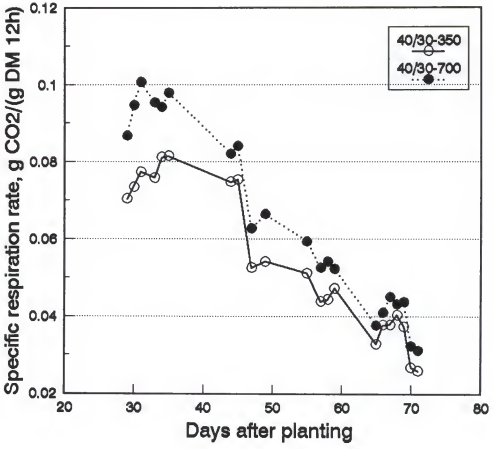


Figure 3-7. The effect of CO_2 on seasonal trend in whole plant specific dark respiration of soybean grown at 40/30 °C in 1994.

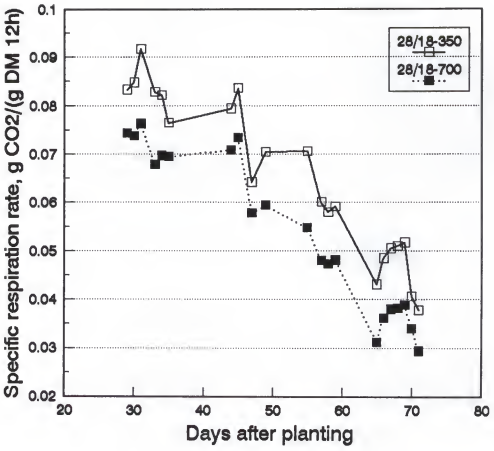


Figure 3-8. The effect of CO_2 on seasonal trend in whole plant specific dark respiration of soybean grown at 28/18 °C in 1994.

anticipated to be stored as non-structural carbohydrates, thus increasing the total dry matter which decreased the calculated specific respiration. Preliminary results of carbohydrate analysis indicate higher total non-structural carbohydrates at the lowest temperature and doubled CO_2 treatments. Temperature acted as a dominant factor affecting dark respiration at doubled CO_2.

Synthesis Efficiency and Maintenance Respiration

The synthesis efficiency (Yg) and maintenance respiration (m) showed that growth respiration increased as the treatment temperature increased (Table 3-2). The difference of growth respiration could possibly result from the difference of development stage caused by the long term temperature treatment. As mentioned before, the difference in plant composition (such as total non-structural carbohydrates) was associated with long term temperature treatments. Plants grown at doubled CO_2 had lower growth respiration. This may be associated with higher non-structural carbohydrate concentration because doubled CO_2 increased total non-carbohydrate in the plants (Allen et al., 1988). This feature was confirmed by preliminary total non-structural carbohydrate analysis of the treatments. Maintenance respiration of the treatment with 36/26 °C was the lowest at doubled CO_2. There was a quadratic shape of maintenance respiration response among the temperature treatments. Doubled CO_2 increased

Table 3-2. Analysis of maintenance respiration (m) and synthesis efficiency (Yg) per unit of soybean plant biomass during 43 to 49 DAP in 1994.

Treatment Temp.-CO_2 °C-μmol mol^{-1}	Yg g CO_2 g CO_2^{-1}	m mg CO_2 g CO_2^{-1} d^{-1}	t-Test
44/34-700	0.63	35	**
40/30-700	0.68	34	**
36/26-700	0.68	29	**
32/22-700	0.74	36	**
28/18-700	0.78	42	**
40/30-350	0.61	24	**
28/18-350	0.73	40	**

** significant at 0.01 level.

Table 3-3. The effect of temperature and CO_2 on nitrogen (N) concentration of soybean leaves and stems sampled at 42 DAP in 1993.

Treatment Temp-CO_2 °C-μmol mol^{-1}	Leaf N g kg^{-1}	Stem N g kg^{-1}
40/30-700	50.2	13.1
36/26-700	47.8	13.6
32/22-700	49.7	13.9
28/18-700	44.4	14.9
40/30-350	52.5	12.5
36/26-350	51.8	12.8
32/22-350	52.2	15.1
28/18-350	52.7	14.3
test on CO_2	**	NS
test on Temp.	NS	*
text on CO_2*Temp		

** *: significant at 0.01, 0.05 level
NS: non-significant

maintenance respiration. It seemed that more nonstructural carbohydrate supply could result in higher maintenance respiration at the same growth temperature.

The analysis of nitrogen concentration of the plants sampled in 1993 showed that leaf nitrogen concentration of the plants grown at doubled CO_2 was significantly lower than that at ambient CO_2 (Table 3-3). Stem nitrogen concentration significantly increased as temperature decreased from 40/30 °C to 28/18 °C at both elevated or ambient CO_2 concentrations; this may be also due to the developmental difference caused by elevated temperature.

Summary

The treatment 36/26 °C, 700 μmol CO_2 mol^{-1} had the highest daily whole plant dark respiration during the vegetative growth phase. Within each treatment, whole plant dark respiration increased linearly with diurnal temperature variation. Seasonal whole plant respiration increased progressively during the first 40 days, stayed high about 30 days, and then gradually decreased as the plant matured and senesced. The changes of seasonal whole plant respiration were similar to those of canopy photosynthesis. Plants grown at elevated temperature had higher specific respiration. The treatment of 36/26 °C, 700 μmol CO_2 mol^{-1} had the lowest specific respiration after 40 DAP. Doubled CO_2 increased specific respiration at 40/30 °C but decreased it at 28/18 °C.

Growth synthesis efficiency (Yg) over 45 to 49 days after planting decreased as treatment temperature increased, and increased at doubled CO_2. Maintenance respiration from 43 to 49 days after planting had quadratic response to temperature treatments at doubled CO_2. The results indicate that doubled CO_2 increases daily total dark respiration as well as photosynthesis. Elevated temperature increased respiration which was proportional to gross photosynthesis and dry matter, therefore, dry matter production may not significantly decrease if a temperature increase occurs.

CHAPTER 4
EFFECTS OF CARBON DIOXIDE AND TEMPERATURE ON EVAPOTRANSPIRATION, CANOPY RESISTANCE AND WATER USE EFFICIENCY

Introduction

The steadily increasing atmospheric CO_2 concentration is mostly attributed to the burning of fossil fuel (Keeling et al., 1988, 1995). Increase of CO_2, methane, nitrous oxide, CFC's and other radiative forcing gases in the atmosphere might cause an increase of surface air temperature (Hansen and Lebedeff, 1987, 1988). The carbon dioxide concentration is projected to double and the mean air temperature is expected to increase in the next century (IPCC, 1990). An important concern is the possible effect of climate change on water requirements for plant growth. Besides more evaporation from water and soil surfaces, an elevated temperature would increase plant transpiration. A large fraction of the terrestrial surface area is covered by plants, therefore, the study of the combined effects of elevated CO_2 and temperature on plant transpiration and water use efficiency is important.

Considerable research on the effect of CO_2 on transpiration has been conducted over the past several decades. The CO_2 effect on plant transpiration is closely related to stomatal response to CO_2. Stomatal opening was found to be decreased by elevated CO_2 concentration and

transpiration rate was therefore decreased (Gaastra 1959; Pallas, J. E., Jr. 1965, Akita and Moss 1972; Kriedemann et al., 1976). Jones et al. (1984) reported that canopy resistance of soybean grown at a 800 μmol CO_2 mol^{-1} treatment was 60% greater than that of a 330 μmol CO_2 mol^{-1} treatment. Cure (1985) reviewed 21 experiments and computed an increase of 51% in stomatal resistance for a doubling CO_2. Leaf temperature was also reported to increase as transpiration was decreased by elevated CO_2 concentration (Gaastra, 1959). Kimball and Idso (1983) reviewed nine CO_2 enrichment experiments and calculated a 34% average reduction of leaf transpiration caused by doubling CO_2. Jones et al. (1985b) found that a soybean canopy at 660 μmol CO_2 mol^{-1} transpired about 10% less water over the season than did the ambient CO_2 canopies. Whole chamber evapotranspiration of prairie grass was reduced by 18%-27% at elevated CO_2 concentration (Bremer et al., 1994). Elevated CO_2 increased water use efficiency of soybean plants (Jones et al., 1985c) and rice plants (Baker et al., 1990). Allen et al. (1994) found that doubled CO_2 increased water use efficiency under both water stressed and unstressed treatments in soybean.

Most of the earlier research was conducted at temperatures lower than 36 °C or short time exposures rather than seasonal exposure to elevated temperatures up to the 44/34 °C (day/night). Short term experiments may not adequately express long term effects. The present study was

initiated to evaluate the effect of doubled CO_2 and elevated temperature on soybean leaf and canopy resistance, evapotranspiration, and water use efficiency, especially under temperatures higher than 35 °C, and to evaluate the effects of potential climate change on the water requirements for plant growth.

Materials and Methods

Two experiments were conducted at the Irrigation Research and Education Park, University of Florida, Gainesville in two seasons, 1993 and 1994. Soybean seeds were sown in eight sunlit, environmentally controlled chambers. The control of daily temperature and vapor pressure is illustrated in Appendix 4, 5 respectively. The other details of the two experiments and the control of the chambers have been described in chapter 2. Most of the evapotranspiration (ET) reported in this research is from temperature response of foliage rather than from soil evaporation. The sub-irrigation system employed supplied root water needs effectively, but the soil surface remained dry except for slight dampness at senescence.

Evapotranspiration

Evapotranspired water was condensed on cooling coils and measured with tipping bucket rain-gauges for each chamber. Collected water was weighed daily during the experiment. The

amount of water per tip was calibrated from total daily water weight and the number of tips recorded by computer during the corresponding time interval. Instantaneous evapotranspiration rates were then calculated as the number of tips per unit time recorded by the computer system multiplied by mole water per tip.

Vapor Pressure Deficit

The calculation for the dependence of saturation vapor pressure on temperature was based on the following formula (Murray,1967):

$$e_s(T) = e_s(T^*)\exp\{A(T-T^*)/(T-T')\}$$

Where $e_s(T)$ is saturation vapor pressure at temperature T in °K. A=17.27, $e_s(T^*)$=0.611 kPa (saturated vapor pressure at T=273 °K), and T'=36 °K.

Saturated vapor pressure (VPs) and actual vapor pressure (VPa) were calculated from the recorded chamber dry bulb temperature and dew point temperature, respectively. Vapor pressure in leaf (VPl) was calculated as saturated vapor pressure at the leaf temperature measured by an infrared thermometer. Vapor pressure deficit (VPD) between the saturated vapor pressure of chamber air and actual vapor pressure of the chamber air at the existing temperature was calculated as the difference between VPs and VPa (Appendix 5). Vapor pressure deficit (VPD_{Leaf}) from inside to outside of the leaf was calculated as the difference between VPl and VPa.

Canopy Resistance

The equation of Monteith (1990) was used to calculate canopy resistance:

$$Rc = \{(\rho * (Mw/Ma)/P\} * \{(e^*_{(Leaf)} - e_{(air)})/ET\}$$

where ET is canopy evapotranspiration (mmol m^{-2} s^{-1}), ρ is air density (mmol m^{-3}), Mw and Ma are the molecular weight of one mole of water and air, P is atmospheric pressure (Pa), $e^*_{(Leaf)}$ is saturated vapor pressure at the leaf temperature (Pa), and $e_{(air)}$ is chamber air vapor pressure at dew point temperature (Pa), and Rc is the canopy resistance to water vapor (s m^{-1}).

Water Use Efficiency

Water use efficiency (WUE) was calculated as the canopy carbon exchange rate (CER: μmol m^{-2} s^{-1}) divided by the canopy evapotranspiration rate (ET: mmol m^{-2} s^{-1}) over the same time interval:

$$WUE = CER/ET$$

Water use efficiency is expressed as μmol CO_2 $mmol^{-1}$ H_2O. Leakage calibration and carbon exchange rate calculations were described in chapter 2.

Stomata Conductance Measured at Leaf Level

The LICOR-6200 portable photosynthesis system was used to measure stomata conductance (LICOR, 1987a, 1987b). Measurements were made at midday during high

photosynthetically-active radiation levels. The leaf cuvette was brought into the growth chamber through a window in the side of the chamber. The measurement was conducted when CO_2 and temperature were equilibrated to the treatment CO_2 and temperature set point for each chamber. The operator used a special breathing mask to remove the exhaled CO_2 to outside air.

Results and Discussion

Leaf Temperatures

Foliage temperature, measured by infrared radiation thermometer in each chamber increased as chamber air temperature increased (Figure 4-1, 4-2). When compared at mid-day the leaf-to-air temperature difference was greater under high temperature than at low temperature (Figure 4-2). Leaf temperature was higher than air temperature when air temperature was less than 31 °C, but it was progressively lower than air temperature as air temperature increased from 31 to 44 °C. Much of this progressive change in leaf-to-air temperature difference can be attributed to increasing transpiration rates associated with increasing VPD as chamber treatment temperature increased.

Doubled CO_2 treatments increased leaf temperatures. Statistical analysis on the data collected from 38 and 43 days after planting in 1993 showed that leaf temperature of the

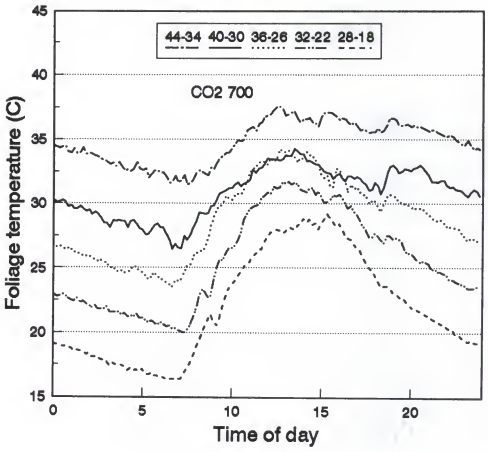


Figure 4-1. Measured foliage temperature at 35 DAP in 1994.

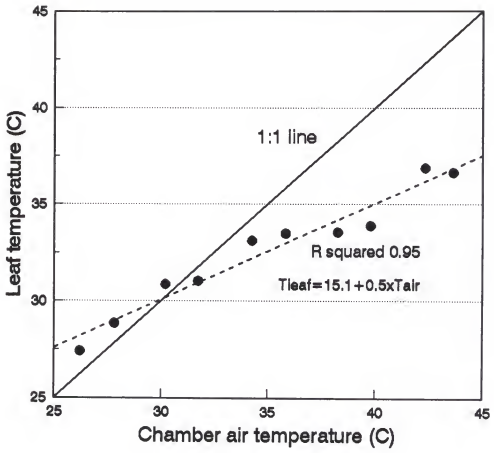


Figure 4-2 The relationship between chamber air temperature and soybean leaf temperature across five temperature treatments at 700 μmol CO_2 mol^{-1}, midday of 35 DAP in 1994.

plants grown at doubled CO_2 concentration was significantly higher than that of the plants grown at ambient CO_2 (Figure 4-3). The increase of leaf temperature was about 0.7-1.4 °C. Other studies have reported leaf temperature increase ranging from 1-3 °C under doubling of CO_2, and that the range depends on species and weather (Choudhury et al., 1986, Idso et al., 1986, 1987). The increase of soybean leaf temperature is at the low end of this range. The mechanism by which CO_2 raised leaf temperature is that doubling CO_2 caused partial stomata closure and increased leaf resistance to water vapor loss. Less leaf transpiration warmed the leaf as less latent heat was lost. This suggests that elevated CO_2 concentration will increase leaf temperature under future possible climate change.

The Relationship Between Leaf-To-Air Temperature Difference and Vapor Pressure Deficit

Vapor pressure deficit (VPD) between the saturated vapor pressure and actual vapor pressure at the chamber air temperature indicates the dryness of the air and therefore is one primary factor that governs evapotranspiration. Allen (1990) reviewed these relationships and suggested that actual data of Tleaf-Tair usually becomes progressively more negative as VPD increases. Jackson et al. (1981) used the relationship between the canopy-to-air temperature difference and vapor pressure deficit to calculate the crop water stress index. Their results showed that there was a good relationship

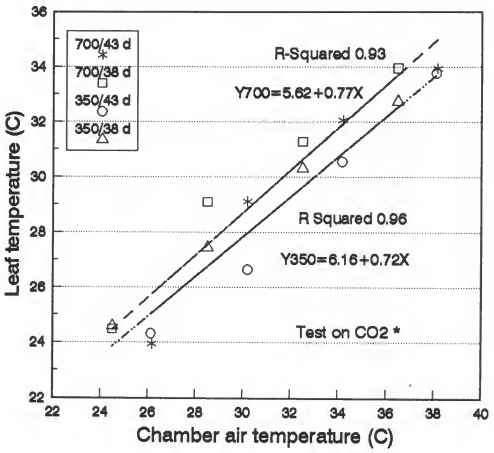


Figure 4-3. The effect of CO_2 on soybean leaf temperature across four levels of temperature treatments at midday of 38 and 43 DAP in 1993.

between canopy-to-air temperature difference and plant water status. Their relationship is used in crop irrigation management. Data across CO_2 and temperature treatments in this experiment showed that temperature difference was a function of vapor pressure deficit and there was a negative linear correlation between them (Figure 4-4). The coefficients and constants changed with total radiation which is important energy source for ET and leaf temperature to change. Photosynthetically active radiation (PAR) is proportional to total radiation. The Y interception and the absolute value of slope increased with PAR (Figure 4-4). Idso (1982) found that the intercept was 1.44 °C and the regression slope was -1.34 °C kPa^{-1} for soybean. The intercept (3.6 °C at 1500 PAR and 6.3 °C at 2000 PAR) and slope (-2.1 °C kPa^{-1} at 1500 PAR and -2.5 °C kPa^{-1} at 2000 PAR) calculated with the data from this experiment had larger absolute values than Idso's (1982), possibly due to PAR difference. The major factor may be that chambers probably have more rapid air exchange, then more transpiration, thus lower leaf temperature and larger leaf-to-air temperature difference at high VPD. Another factor is that plants in the SPAR chambers had a cover over the top which provided more thermal radiation than from the clear sky. The slope of double CO_2 treatment was very close to that of ambient CO_2 treatment at the same PAR in 1993 (Figure 4-5), but the Y intercept was about 2 °C higher for the doubled CO_2 treatment because doubled CO_2 concentration caused partial

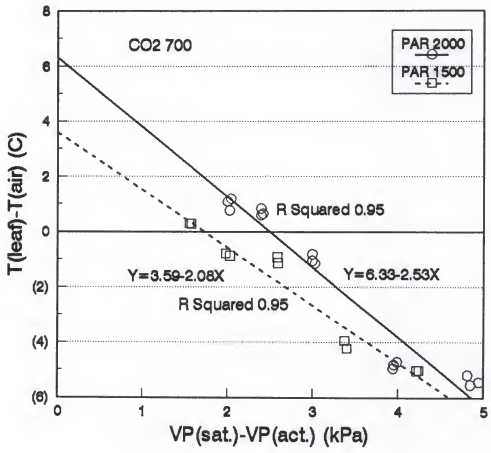


Figure 4-4. The relationship between soybean leaf-to-air temperature difference and vapor pressure deficit across five temperature treatments at 700 μmol CO_2 mol^{-1} at 35 DAP in 1994.

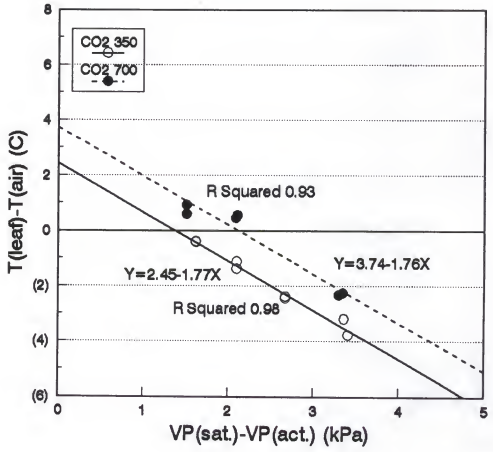


Figure 4-5. The relationship between soybean leaf-to-air temperature difference and vapor pressure deficit across four levels of temperatures and two levels of CO_2 at 1770 μmol PAR m^{-2} s^{-1} at 38 DAP in 1993.

stomata closure, less transpiration and resulted in higher leaf temperatures by 1 to 1.5 °C. Results indicated that higher temperature treatments had higher driving force of transpiration because of higher leaf-to-air temperature difference and vapor pressure deficit (Figure 4-4, 4-5). Elevated temperature caused more transpiration from plants and lower water use efficiency in comparison with normal temperatures.

Leaf Stomatal Conductance and Canopy Resistance

Leaf stomatal conductance

Stomata conductance measured at the leaf level is a quantitative measure of stomatal opening. Statistical analysis of stomatal conductance to CO_2 indicated that stomatal conductance values at high PAR were positively correlated with leaf temperatures and negatively correlated with CO_2 concentrations (Table 4-1). The interaction of temperature and CO_2 was not significant. Leaf resistance calculated with the equation from regression analysis showed that the leaf resistance ratio of doubled CO_2 treatment to ambient CO_2 treatment decreased with increasing temperature (Table 4-2). The CO_2-induced decrease in leaf conductance to CO_2 was 33% at 27 °C and 17% at 40 °C. Leaf resistance to CO_2 increased 48% at 27 °C and increased 20% at 40 °C by doubled CO_2. This indicates that stomatal response to CO_2 varied with temperature. The effect of elevated CO_2 on leaf resistance to CO_2 was much less

Table 4-1. Regression analysis of CO_2 (CO2) and leaf temperature (Tleaf) effects on soybean leaf stomatal conductance (g) to CO_2 at 63 and 67 DAP in 1993, and at 24 and 47 DAP in 1994.

Parameter	Estimated values	Test
a	0.041	**
b	-0.00052	**
c		NS

**: significant at 0.01 level, NS: non-significant
Tleaf range: 27/41 °C; CO2: 350 & 700 μmol mol^{-1}
g = a*Tleaf + b*CO2 + c*Tleaf*CO2 + d (cm s^{-1}), N=96

Table 4-2. Effect of doubled CO_2 on leaf conductance (g) and leaf resistance (R) to CO_2 calculated with equation from Table 1.

Leaf temp.	g700/g350	R700/R350	under doubled CO_2 g change	R change
°C	-------ratio-------		-------%------	
27	0.67	1.48	-33	+48
30	0.73	1.37	-27	+37
35	0.79	1.26	-21	+26
40	0.83	1.20	-17	+20

at high temperature. Cure (1985) reviewed 21 experiments and computed a decrease of 31±5% in stomatal conductance of soybean for a doubling of CO_2 concentration. Morison (1987) reviewed 23 reports with different species and found a 64±14% increase in stomatal resistance at 660 μmol mol^{-1} in comparison with 330 μmol mol^{-1}. Thus, doubled CO_2 may increase stomatal resistance by about half on average at temperature lower than 36 °C although results in this study indicate less effect at temperature higher than 36 °C.

Canopy resistance

Canopy resistance to water vapor at 700 μmol CO_2 mol^{-1} decreased as treatment temperature increased (Figure 4-6). Lower canopy resistance at higher temperature was mainly caused by a higher ET via a larger leaf area index. Canopy resistance was also affected by PAR because it is a major driving force for water loss and for CO_2 concentration change in guard cells. Elevated temperature decreased canopy resistance to water vapor loss, and was associated with high ET. Part of the diurnal response of canopy resistance must also be attributed to diurnal temperature changes in the chambers, because lowest resistance occurred near 15 hours when temperature peaked. Canopy resistance was greater with doubled CO_2 for the 28/18 °C treatment (Figure 4-7), but there was no CO_2 effect for the 40/30 °C treatment. The CO_2 effect on canopy resistance was much less at high temperature. The same phenomenon was observed for leaf resistance to CO_2

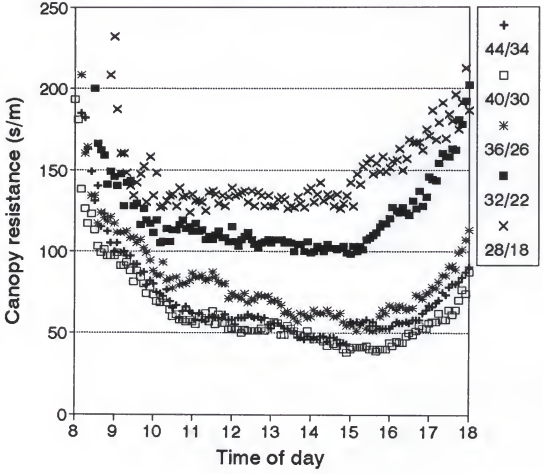


Figure 4-6. The effect of temperature treatments on diurnal soybean canopy resistance at 700 μmol CO_2 mol^{-1} at 35 DAP in 1994.

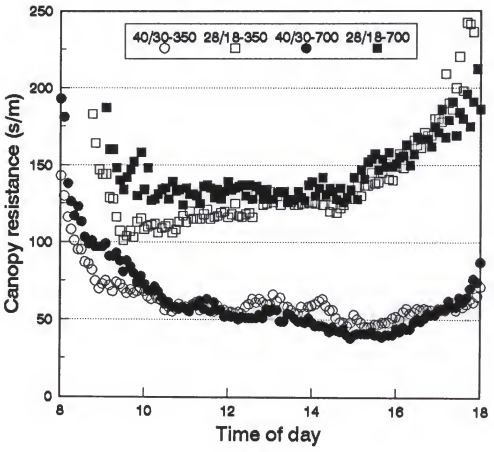


Figure 4-7. The effect of CO_2 and temperature treatments on diurnal soybean canopy resistance at 35 DAP in 1994.

measured independently with the LICOR Steady State Photosynthesis System. Canopy resistance varied during the soybean life cycle as leaf area index initially increased and then as leaf senescence progressed at the end of the season (Figure 4-8). In the middle of growing season, canopy resistance was the lowest and also associated with the highest ET. Temperature treatment effects were apparent for the entire season. Elevated CO_2 increased canopy resistance at the 28/18 °C temperature treatment but canopy resistance of doubled CO_2 treatment was very similar to the ambient CO_2 treatment at 40/30 °C (Figure 4-9). If the canopy resistance is divided by leaf area index, the effective single leaf resistance is found to be decreased by elevated CO_2 at 28/18 °C, but not significantly affected by CO_2 at 40/30 °C. The results indicated that temperature at 40/30 °C or higher could offset the effect of CO_2 on canopy resistance.

Evapotranspiration

Instantaneous ET increased with PAR (Figure 4-10), but showed a 2-hour lag associated with peak temperature of the diurnal temperature treatment cycle. The ET also increased with treatment temperature. Both PAR and chamber temperature were energy sources for the leaf water to evaporate. It appears that temperature treatments above 32/22 °C had substantial heat energy input, because of considerable ET at sunrise for these treatments. The treatments with temperature

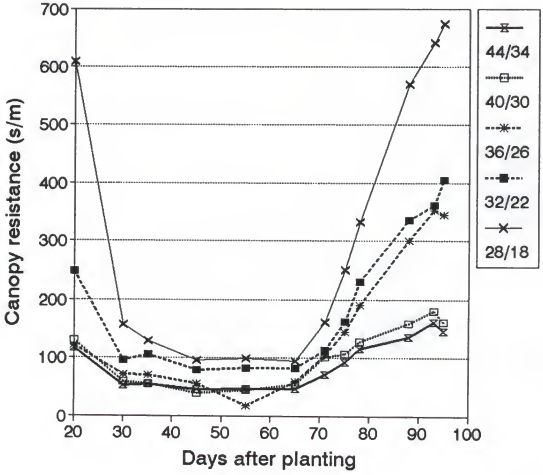


Figure 4-8. The effect of temperature treatments on seasonal change of soybean canopy resistance at 700 μmol CO_2 mol^{-1} in 1994.

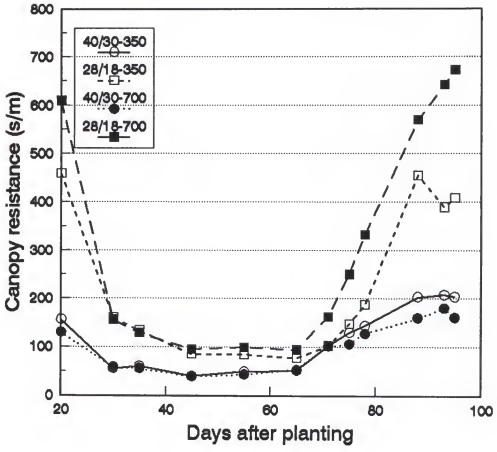


Figure 4-9. The effect of CO_2 and temperature treatments on seasonal change of soybean canopy resistance in 1994.

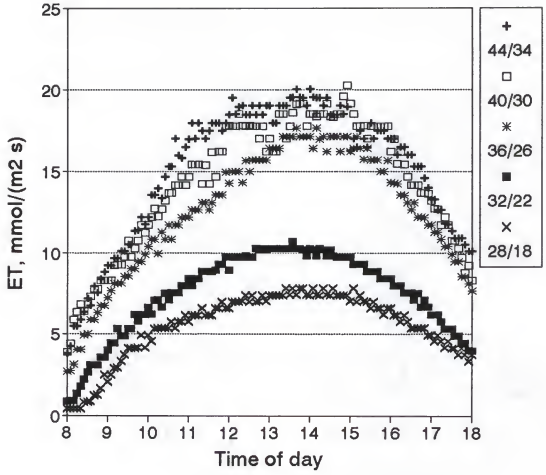


Figure 4-10. The effect of temperature treatments on diurnal soybean evapotranspiration at 700 μmol CO_2 mol^{-1} at 35 DAP in 1994.

of 44/34 and 40/30 °C had high ET values that were similar. This is because the leaf area index of the 44/34 °C treatment was less than that of the 40/30 °C treatment at 35 days after planting in 1994. On the other hand, high air temperature such as 44 °C caused slight leaf wilt at midday with high PAR. This implies that the potential amount of water transpired in the 44/34 °C treatment was larger than that which the plant roots could absorb from soil. Elevated CO_2 caused lower ET for the 28/18 °C treatments, but the effect of elevated CO_2 on ET was much less at 40/30 °C treatment (Figure 4-11).

Total daytime ET from 8:00 to 18:00 hours peaked at the middle of the growing season, because the LAI was the highest at that time (Figure 4-12). Total ET also increased with treatment temperature. Plants treated with 44/34 °C had lower ET initially than those treated with 40/30 °C because of slower early leaf area development. Subsequently, the 44/34 °C treatment had the highest ET because it developed the greatest leaf area index and had the highest temperature. As the leaf area index continued to increase during the experiment, ET from the 44/34 °C treatment became much larger than that from the 40/30 °C treatment.

Although leaf area index of the doubled CO_2 treatment was higher than that of the ambient CO_2 treatment, transpiration from the ambient CO_2 treatment was higher than that of the doubled CO_2 treatment at 28/18 °C (Figure 4-13). Transpiration rate per unit leaf area for ambient CO_2 treatment was higher

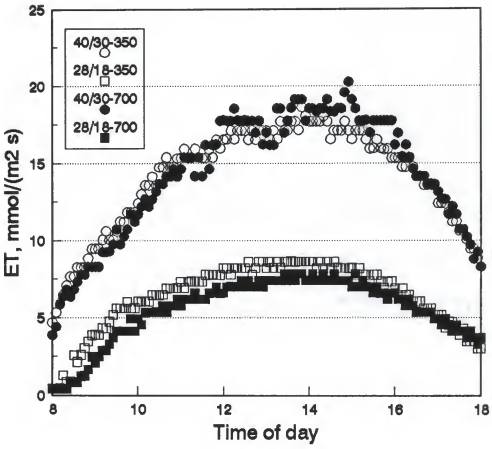


Figure 4-11. The effect of CO_2 and temperature treatments on diurnal soybean evapotranspiration at 35 DAP in 1994.

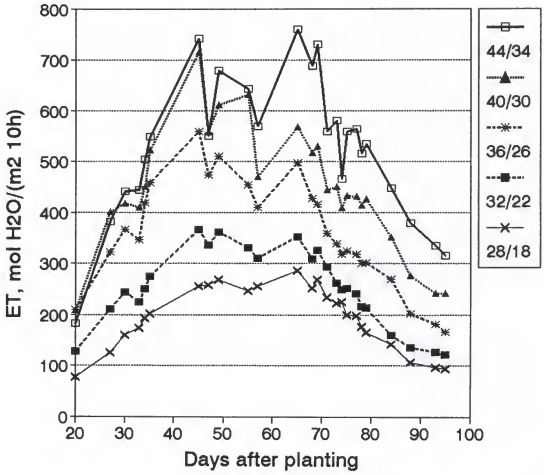


Figure 4-12. The effect of temperature treatments on seasonal course of daily soybean evapotranspiration at 700 μmol CO_2 mol^{-1} in 1994.

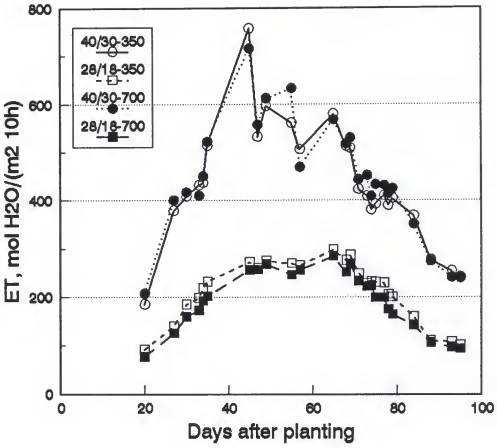


Figure 4-13. The effect of CO_2 and temperature treatments on seasonal course of daily soybean evapotranspiration in 1994.

than that for doubled CO_2 treatment. Cure (1986) calculated a 23% decrease of leaf transpiration on the basis of 19 reports for soybean at doubled CO_2. The decreased ET for temperature lower than 36/26 °C was comparable to Cure's values. ET data (Figure 4-14) obtained by averaging the value of total ET for 25 days in 1994 (Figure 4-12 & 4-13) also showed that there was much less CO_2 effect on ET at 40/30 °C. ET linearly correlated with chamber air VPD (Figure 4-15), because VPD is also a function of temperature. Therefore, temperature acted as the primary determinator of ET. The extent of the decrease of ET by CO_2 appeared to be offset by the effect of elevated temperature and more water would be needed for physiological and ecological requirement at high temperature. ET is expected to increase at elevated temperatures even if CO_2 is doubled, especially in the tropical regions where the maximum air temperature is relatively high. This experiment confirmed the conclusion by Allen et al. (1985) who suggested that both the increased crop leaf area and the increased foliage temperature at doubled CO_2 tend to offset reductions in crop transpiration that might be expected from elevated CO_2. If global temperature rises with increasing CO_2, future crop water use may actually increase.

Water-Use Efficiency

Instantaneous water-use efficiency (WUE) decreased with time of day under doubled CO_2 (Figure 4-16). In the morning,

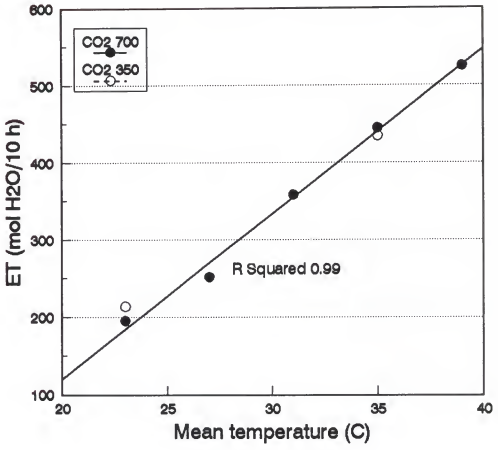


Figure 4-14. The effect of CO_2 and temperature treatments on the mean of 25 days of daily soybean evapotranspiration in 1994.

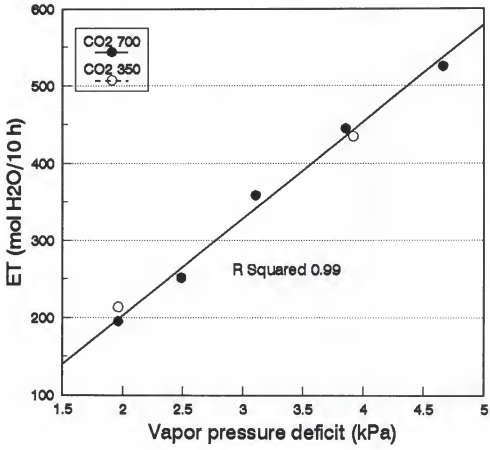


Figure 4-15. The effect of chamber air vapor pressure deficit on evapotranspiration of soybean in 1994.

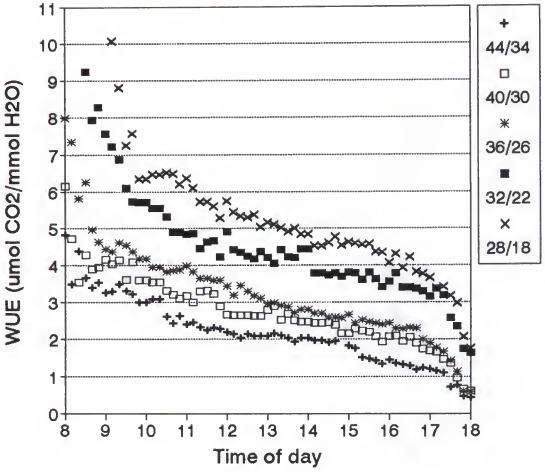


Figure 4-16. The effect of temperature treatments on diurnal soybean water-use efficiency at 700 μmol CO_2 mol^{-1} at 35 DAP in 1994.

gross photosynthesis and ET both increased as the sun was rising, but the increase in ET was greater than that of photosynthesis. In the afternoon, photosynthesis decreased as the PAR decreased, but chamber air temperatures and vapor press deficit were still relatively high (the maximum diurnal temperature was set at 15:00 hours EST), therefore, ET did not decrease as soon as photosynthesis, and thus WUE kept decreasing.

WUE decreased as treatment temperature increased. This was mainly attributed to the increase of ET and VPD under higher temperature. Doubled CO_2 treatments increased WUE (Figure 4-17). This was mainly due to the increase of photosynthesis and slight decrease of ET at doubled CO_2.

Although the 36/26 and 40/30 °C treatments had the highest canopy photosynthetic rate, their seasonal evapotranspiration was much higher than that of the lower temperature treatments. Therefore, seasonal WUE at 36/26 and 40/30 °C was lower than that at 32/22 and 28/18 °C. The 44/34 °C treatment had the highest ET. WUE decreased as the treatment temperature increased (Figure 4-18). Doubled CO_2 caused higher canopy photosynthesis and therefore resulted in higher seasonal WUE in comparison with ambient CO_2 (Figure 4-19).

Soybean total dry matter increased about 55% and seed yield increased 30% at doubling CO_2 on the basis of experiment results in 1993 and 1994. If mean global air temperature

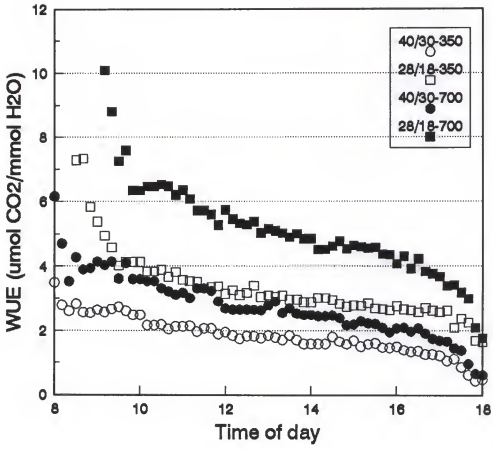


Figure 4-17. The effect of CO_2 and temperature treatments on diurnal soybean water-use efficiency at 35 DAP in 1994.

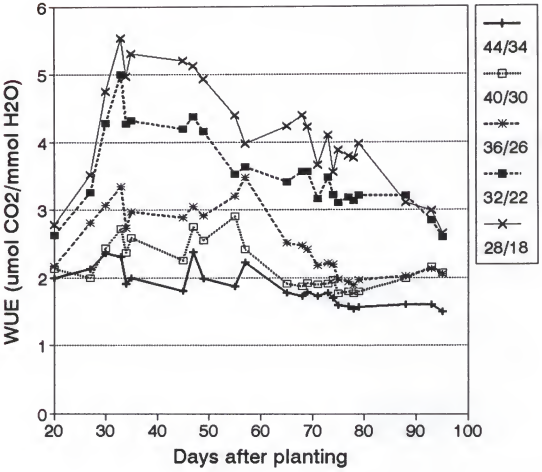


Figure 4-18. The effect of temperature treatments on seasonal course of daily soybean water use efficiency at 700 μmol CO_2 mol^{-1} in 1994.

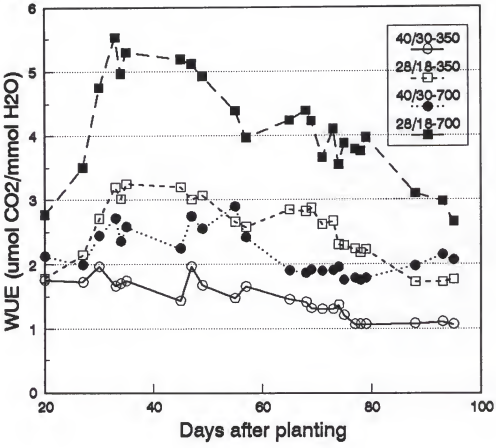


Figure 4-19. The effect of CO_2 and temperature treatments on seasonal course of daily soybean water-use efficiency in 1994.

increases, seed yield enhancement by elevated CO_2 could be less than the yield loss caused by elevated temperature (see chapter 5). High temperature did not significantly reduce photosynthesis, but it did cause lower reproductive fertility, higher abortion of pods and smaller seeds. From an economic point of view, elevated temperature would cause more water requirement for plant growth, thus only cool regions would benefit if climate change occurs. High cost for water, and lower water use efficiency for yield could cause problems in high temperature regions such as the tropics.

Summary

Instantaneous and daily canopy ET increased as treatment temperature increased. Doubled CO_2 decreased canopy ET, but there was little CO_2 effect on ET when mean air temperature was 35 °C or higher. Ranges of ET can be explained by its driving force and stomata opening. Leaf temperature increased with increasing air temperature. Doubled CO_2 also increased leaf temperature about 1.5 °C for soybean plants. Leaf-to-air temperature difference was negatively correlated with vapor pressure deficit of the air. Leaf-to-air temperature difference decreased as vapor pressure deficit increased. Elevated temperature caused a higher driving force for ET through greater vapor pressure deficit. Leaf resistance to CO_2 or canopy resistance to water vapor increased with increasing CO_2 concentration but decreased as air temperature increased.

The CO_2 effect on leaf or canopy resistance was much less when daily mean temperature reached 35 °C. Water-use efficiency was increased under doubled CO_2 concentration and decreased with elevated temperature. ET is expected to increase in warm regions if climate change occurs.

CHAPTER 5
EFFECT OF ELEVATED CO_2 AND TEMPERATURE ON SOYBEAN GROWTH AND DEVELOPMENT

Introduction

The greenhouse effect (Plass, 1956; Kaplan, 1960; Moller, 1963) and the increase of greenhouse gases and air temperature during the last century (Brown & Keeling, 1965; Pales & Keeling, 1965; Jones, 1986; Keeling et al., 1989; Hansen and Lebedeff, 1987,1988) have aroused concerns for effect of elevated CO_2 and temperature on crop production.

Allen (1979), Kimball (1983), Acock and Allen et al. (1985), Cure and Acock (1986), and Allen (1990b) have reviewed plant responses to elevated CO_2 including soybean. There was little effect of CO_2 on phenology dates such as flowering and maturity of soybean (Cooper and Brun, 1967). The rate of main stem development was either not affected (Jones et al., 1984a) or slightly increased by elevated CO_2 (Allen et al., 1990). Vegetative growth rate was greater and all size parameters were increased at elevated CO_2 concentration (Allen et al., 1990; Allen, 1990). Extensive experiments have been done on soybean growth responses to CO_2 (Allen et al., 1991; Baker et al., 1989; Cooper and Brun, 1967; Hardman and Brun, 1971; Havelka et al., 1984; Finn and Brun, 1982; Jones et al.,

1984a; and Rogers et al., 1984). In general, elevated carbon dioxide significantly increased dry matter accumulation by soybean plants, but dry matter partitioning was changed little. The degree of dry matter increase varied with CO_2 concentrations. Plant height, number of nodes and branches were increased. Both leaf area index and specific leaf weight increased. Baker et al. (1989) reported that both elevated CO_2 and temperature increased seed number. The yield increase with CO_2 was mainly attributed to the increased number of pods and seed instead of individual seed weight. Generally speaking, the yield increased by one-third with doubled CO_2 (Kimball, 1983; Allen et al., 1988).

There have been few soybean experiments conducted on the combined effects of both elevated CO_2 and elevated temperature. Most of the previous experiments mainly focused on the effect of carbon dioxide enrichment at air temperature of 20-35 °C, such as Sionit (1987a, 1987b). Cotton boll production was reported to be sharply decreased by elevated temperature (Reddy et al., 1991a, 1991b). Rice and wheat reproduction were also reported to be very sensitive to temperature; high temperature reduced the seed filling duration and the percentage of filled seeds, and caused low yields (Baker et al., 1992a, 1992b; Tashiro and Wardlaw, 1989). Even elevated CO_2 reduced rice duration of development (Baker et al., 1990a). It is very important to understand elevated temperature effects on growth responses because

elevated temperature may reduce seed yields even while vegetative growth is unaffected. The objective of this experiment was to determine the combined effects of doubled CO_2 and elevated temperature on soybean growth, development and seed production.

Materials and Methods

Plant Culture

Soybean [*Glycine max* (L.) Merr.] c.v. Bragg plants were grown at Gainesville, Florida from sowing to maturity in sunlit, computer-managed and environment-controlled chambers. Carbon dioxide concentrations, treatment temperatures and the control of the chamber system is described in Chapter 2. Seeds were inoculated with *Brady-rhizobium* just before planting. Soil used for the chambers was a reconstructed Kendrick fine sand (loamy, siliceous, hyperthermic Grossarenic Paleudult). Magnesium sulfate was applied at the rate of 34 gram per square meter and incorporated into the top 15 cm of soil. To control rootknot nematodes, soil was treated with Nemacur at the rate of 4.48 g m^{-2} (0.672 g active ingredient m^{-2}) and mixed in the 15 cm of top soil. Soybean seeds were sown on 19 August, 1993 and 11 February, 1994 respectively, using a 33-cm row spacing.

Sampling

Soybean plants were thinned to 75 plants m^{-2} at 11 days after planting (DAP). Plant sampling was conducted weekly in earlier months and biweekly in later months (Table 5-1). The sampled plants were separated into leaves (leaf blades), stems (including petioles) and pods. Vegetative stage and reproductive stages were recorded as described by Fehr et al. (1971). Leaf area was measured with a LI-COR LI-3100 leaf area meter. Separated plant parts were microwaved for 1 to 3 minutes depending on sample size, and then dried at 70 °C for more than 48 hours until completely dried. Pods were tagged at the R3 stage in each chamber. Pods were sampled weekly after the R3 stage and the pod wall and seeds were separated and dried at 70 °C for 48 hours. The individual seed growth rates of tagged pods were therefore determined. The effective filling period is calculated as the ratio of the final weight divided by seed growth rate. Final-harvest pods and seeds were air-dried. The water content of air-dried seeds was 10%.

Data Analysis

Three plant sub-samples were taken from each chamber. The three replicates corresponded to plants sampled from rows 1-2, rows 3-4 and rows 5-6. Plants were taken at random within each replicate region. The General Linear Model (GLM) as described in the SAS user's Guide (SAS Institute Inc., 1987) was used for the statistical analyses. Experimental data at five

temperature levels and doubled CO_2 were used for temperature effect analysis, and those at two levels of temperature and two levels of CO_2 were used for CO_2 effect analysis.

Results and Discussion

Reproductive Development and Life Cycle

Temperature affected soybean reproductive development (Table 5-2). There was quadratic relationship between the days from planting to flowering and treatment temperatures. The optimum daily mean temperature for the development from planting to flowering (R1) was between 27 to 31 °C (32/22 and 36/26 °C treatments). Lower or higher temperature prolonged the time to flower. The largest difference from planting to flowering among the treatments was 7 days except the 48/38 °C treatment. The variation in time from planting to physiological maturity among the treatments was 30 days. The treatments from 28/18 to 36/26 °C reached the R8 stage, but the 40/30 and 44/34 °C treatments still had not reached physiological maturity when the experiment ended at 110 DAP. The duration from flowering to physiological maturity increased with temperature. This appeared to be different from some cereal crops such as wheat and rice in which higher temperature shortened the duration from flowering to physiological maturity (Tashiro and Wardlaw, 1989). Temperatures above 23 °C mean temperature (28/18 °C) progressively prolonged the soybean seed development and

Table 5-1. The number of soybean plants sampled and remaining after sampling in 1994.

Sampling day		Sampled	Remaining
DAP	JDAY	plant/m^2	plant/m^2
11	58	24	75
18	59	9	66
25	66	9	57
32	73	6	51
39	80	6	45
46	87	6	39
53	94	6	33
71	112	6	27
85	126	6	21

Table 5-2. Effect of CO_2 and temperature treatments on final mean leaf number on the main axis (n=24) and reproductive stages in 1994.

Temp.-CO_2	Final leaf	R1	R3	R4	R5	R6	R7	R8
°C-μmol mol^{-1}	-- No --	---------- DAP ----------						
48/38-700		37#	-	-	-	-	-	-
44/34-700	11.3±0.1	34	67	71	77	-	-	-
40/30-700	9.0±0.2	28	38	43	48	67	93	125@
36/26-700	8.3±0.1	26	34	38	42	56	82	110
32/22-700	7.8±0.2	27	33	36	40	54	78	95
28/18-700	7.5±0.1	33	37	41	44	61	79	95
40/30-350	8.5±0.1	28	39	45	48	68	94	125@
28/18-350	7.0±0.2	33	37	41	44	61	79	95
CO2	**	NS						
TEMP (quadratic)	**	**						
CO2*TEMP	NS	NS						

** significant at 0.01 level, NS non-significant
# plants at edge rows only @ estimated
- plants did not reach this stage at harvest time

filling phases. The mechanism by which high temperature prolongs the growth duration is not completely understood. Elevated CO_2 did not significantly affect reproductive growth duration of soybean.

If elevated temperature prolongs the days from planting to harvest, it could cause more water to be required for growth, and more cost for water use even if temperature does not cause yield to decrease. The reduced dry matter partitioning to seed, and low seed yield at elevated temperature is an even more important problem.

Leaf Area Growth

For the first 40 days, leaf area growth under doubled CO_2 was most rapid at 36/26 °C, followed by 40/30 and 44/34 °C (Figure 5-1). The 28/18 °C treatment had a considerably longer lag phase in leaf area development. Leaf area peaked later at a higher maximum for the 44/34 °C treatments, because flowering and pod formation were greatly reduced and available assimilates were used for continued leaf growth. Peak leaf area occurring during the reproductive phase was progressively increased by temperature increase from 28/18 up to 44/34 °C. The larger total leaf area under elevated temperature was attributed to larger area per leaf on the main stem (Figure 5-2), and to increased total branch leaf area from 28/18 up to 44/34 °C (Figure 5-3). Doubled CO_2 treatment promoted leaf growth for the 28/18 °C treatment but had no significant

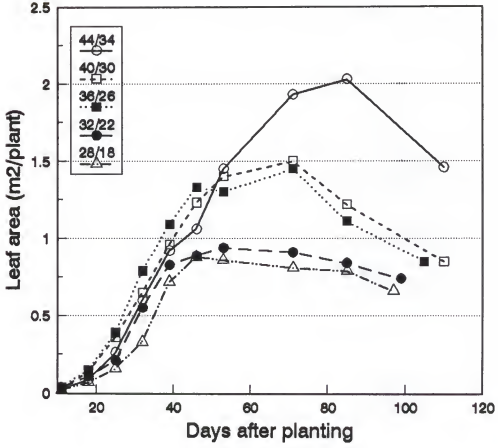


Figure 5-1. Effect of growth temperature on seasonal course of leaf area per plant at 700 μmol CO_2 mol^{-1} in 1994.

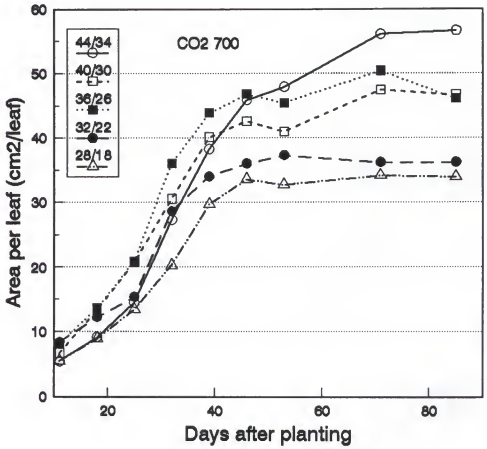


Figure 5-2. Effect of growth temperature on seasonal course of the area per leaf at 700 μmol CO_2 mol^{-1} in 1994.

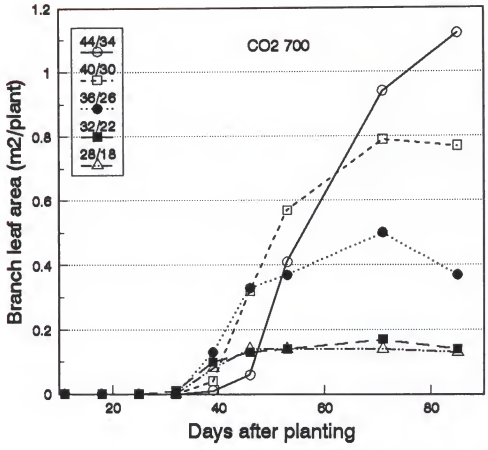


Figure 5-3. Effect of growth temperature on seasonal course of branch leaf area at 700 μmol CO_2 mol^{-1} in 1994.

effect at 40/30 °C (Figure 5-4). This was associated with no CO_2 effect on main stem leaf size at 40/30 °C (Figure 5-5) although there was an increase of total branch leaf area for doubled CO_2 treatment at 40/30 °C (Figure 5-6). The effect of CO_2 on leaf growth was less at 40/30 °C. Temperature acted as a dominating factor affecting leaf area growth.

As temperature increased, a greater total number of leaves were produced on the main axis (Table 5-2). There were two reasons for this response. First, rate of leaf appearance was accelerated as temperature increased from 28/18 up to 44/34 °C. Secondly, time to flower (R1) and time to beginning pod (R3) were delayed as temperature increased from 32/22 to 44/34 °C. The longer time to initiation of reproductive growth allowed more nodes to be initiated and eventually expressed. Thus, elevated temperature increased total leaf area per plant because of increased leaf number on the main axis, increased leaf size, and increased total branch leaf area. Doubling CO_2 also increased final leaf number significantly, but by only a small amount (0.5 nodes). This small increase of 0.5 nodes could be attributed to both increased assimilate supply and somewhat higher (1 °C) foliage temperature at doubled CO_2. The relationship between leaf area per plant and treatment temperature was quadratic during the vegetative growth phase and linear during reproductive growth phase (Table 5-3). Elevated temperature had adverse effects on fertility and pod/seed growth, and caused more leaf growth for high

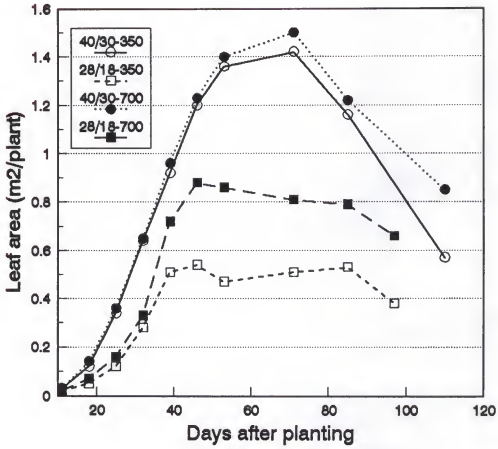


Figure 5-4. Effect of growth temperature and CO_2 on seasonal course of leaf area per plant in 1994.

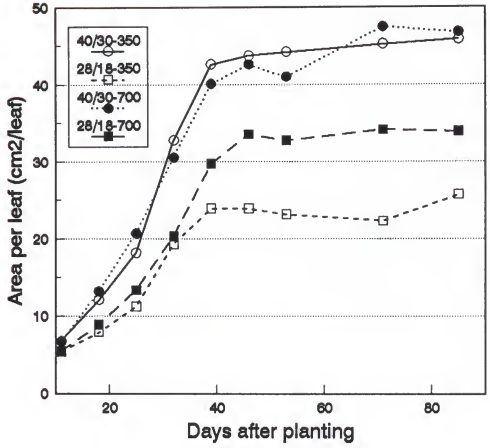


Figure 5-5. Effect of growth temperature and CO_2 on seasonal course of area per leaf in 1994.

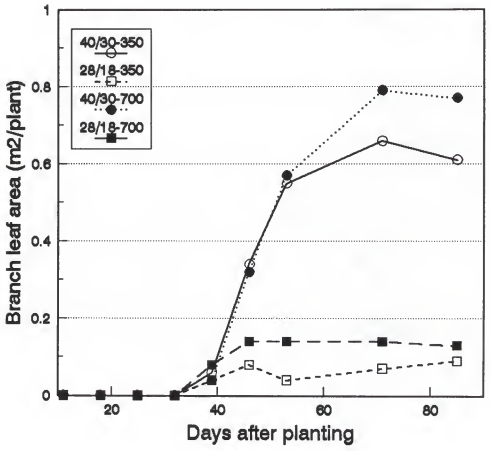


Figure 5-6. Effect of growth temperature and CO_2 on seasonal course of branch leaf area in 1994.

Table 5-3. Temperature and CO_2 effects on leaf area per plant at different DAP.

DAP	Temp. effects		CO_2 effects	
	Quadratic	Linear	28/18°C	40/30°C
	(GLM)		(t-test)	
25	**	NS	**	NS
39	*	*	**	NS
53	NS	*	**	NS
71	NS	**	**	NS

** * Significant at 0.01 and 0.05 level
NS non-significant

temperature treatments. A CO_2 effect on leaf area growth was significant at 28/18 °C but not significant at 40/30 °C. This confirmed the importance of temperature on leaf growth.

Specific leaf weight (SLW) increased over time for all treatments (Figure 5-7 and Figure 5-8). The SLW was generally the greatest for the lowest temperature treatments (28/18 °C, followed by 32/22 °C during the vegetative phase). However, the SLW for the 44/34 °C treatment was also high, particularly late in the life cycle. It appears that the optimum temperature for rate of leaf area growth (36/26 °C) is the temperature at which SLW is generally the lowest. On the other hand, at non-optimum temperatures (either too low or too high), SLW is increased. The very high SLW of the 44/34 °C treatment at 85 days after planting is associated with failure of reproductive site formation and subsequent retention or allocation of assimilates to leaves and stems. Doubled CO_2 concentration significantly increased SLW at both low and high temperatures. Increased SLW with elevated CO_2 is commonly

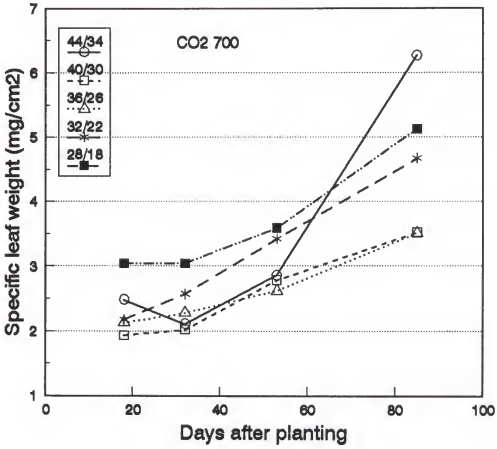


Figure 5-7. Effect of growth temperature on seasonal course of specific leaf weight at 700 μmol CO_2 mol^{-1} in 1994.

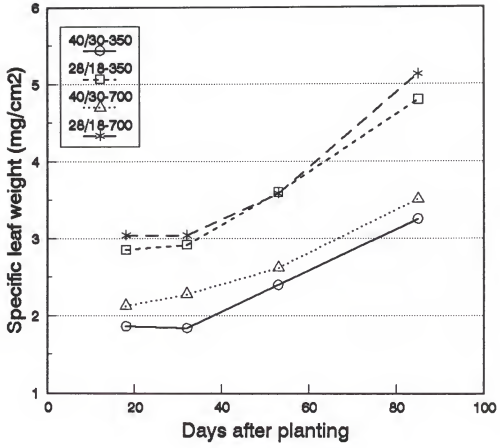


Figure 5-8. Effect of growth temperature and CO_2 on seasonal course of specific leaf weight in 1994.

observed with higher leaf density and more layers of mesophyll palisade cells (Thomas and Harvery, 1983; Vu et al., 1989).

Dry Matter Partitioning, Accumulation and Plant Height

Total dry matter accumulation per plant over time was greatest for the 36/26 °C treatment (Figure 5-9). This treatment also had the largest total dry matter per plant at final harvest (Table 5-4). Although the 36/26 °C treatment appeared to be the optimum temperature for dry matter accumulation, the temperature effect on total dry matter accumulation at 700 μmol mol^{-1} was not statistically significant. Doubled CO_2 significantly increased total dry matter (Table 5-4 and Figure 5-10). On average, doubled CO_2 increased total dry matter by 55% in 1994 (Table 5-4). There was no interaction between CO_2 and temperature. The results are very similar to rice responses reported by Baker et al. (1992a). Leaf dry matter as a fraction of total plant dry matter (fraction leaf), declined with days after planting (Figure 5-11). Fraction stem increased with time until pod formation began at 40 DAP (Figure 5-12). The time series shift in the cumulative fraction leaf or fraction stem are the results of daily partitioning of assimilates to plant parts. The 36/26 °C treatment had the lowest fraction leaf on any given date, whereas the two coolest treatments (28/18 and 32/22 °C) had higher fraction leaf than other treatment except for the 44/34 °C treatment after 40 DAP. Likewise, the 36/26

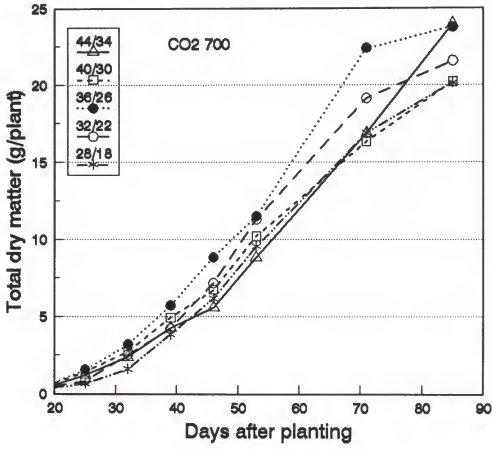


Figure 5-9. Effect of growth temperature on seasonal course of dry matter accumulation at 700 μmol CO_2 mol^{-1} in 1994.

Table 5-4. Effect of temperature and CO_2 treatments on harvested total above-ground dry matter (DM), final plant height and effective filling period (EFP) of seed in 1994.

Temp.-CO_2	Total DM	Plant height	EFP
°C-μmol mol^{-1}	g/plant	cm	days
44/34-700	26.1	62.2	61
40/30-700	25.5	63.7	56
36/26-700	27.1	64.9	46
32/22-700	24.1	50.8	41
28/18-700	23.0	43.4	38
40/30-350	16.6	56.6	54
28/18-350	15.1	34.9	40
CO2	**	**	NS
TEMP.	NS	**Q	**L
CO2*TEMP.	NS	NS	NS

** significant at 0.01 level, NS non-significant
Q quadratic L linear

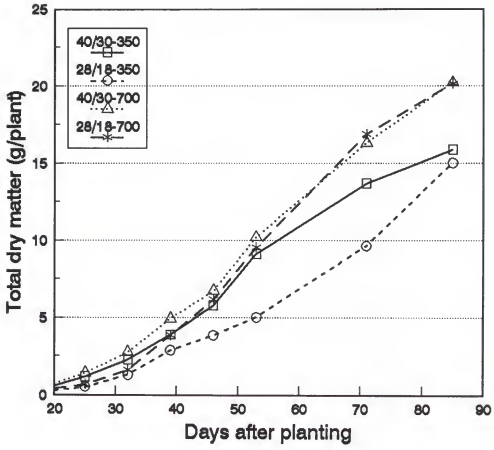


Figure 5-10. Effect of growth temperature and CO_2 on seasonal course of dry matter accumulation in 1994.

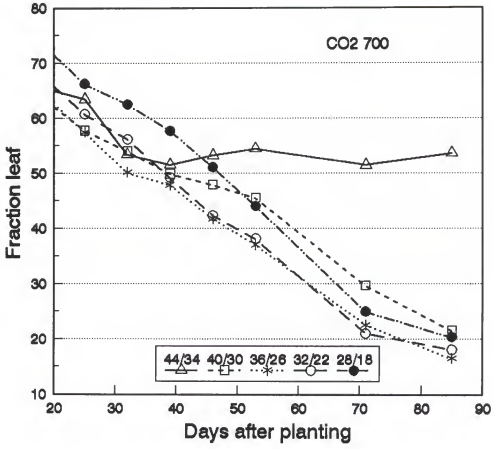


Figure 5-11. Effect of growth temperature on seasonal course of fraction leaf at 700 μmol CO_2 mol^{-1} in 1994.

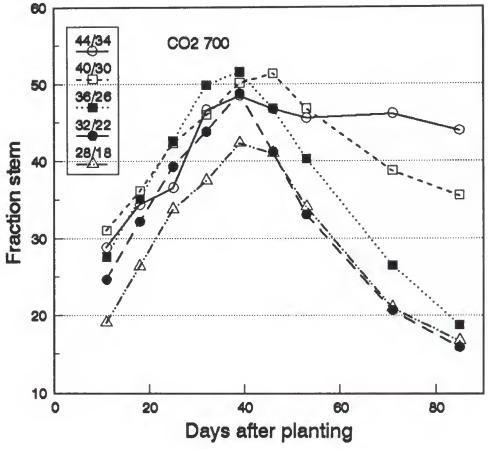


Figure 5-12. Effect of growth temperature on seasonal course of fraction stem at 700 μmol CO_2 mol^{-1} in 1994.

°C treatment had the highest fraction stem until 40 DAP, and the cooler treatments (28/18 and 32/22 °C) had lower fraction stem on those same dates. Recall that the 36/26 °C treatment had the greatest leaf area growth, lowest SLW, and high dry matter accumulation. It appears that 36/26 °C is the optimum temperature for export of assimilates from leaf tissue (to give low SLW) and also optimum for growth of all other tissues including stems. For the 44/34 °C treatment, the sustained fraction leaf and fraction stem over time were caused by failure of reproductive growth. At 44/34 °C treatment, few seeds formed, seeds grew very slowly and seed size was small which resulted in more available assimilate for sustained stem and leaf growth. The effect was less severe for the 40/30 °C treatment, and was the cause for fraction stem and fraction leaf to remain higher than cooler treatments. Doubled CO_2 increased fraction stem (Figure 5-13); it seems that more carbohydrates produced by elevated CO_2 are stored in stems.

Fraction pod (cumulative fraction of total plant dry matter in pod plus seed) increased linearly with time for most treatments (Figure 5-14). Fraction pod was highest for the 32/22 °C treatment, although 36/26 °C flowered one day earlier. The 36/26 and 28/18 °C treatments had similar fraction pod. The fraction pod at 40/30 and 44/34 °C treatments was proportionally much smaller than that of the other three treatments. Elevated temperature (40/30 and 44/34 °C) caused low fraction pod because of fewer pods, smaller and slower

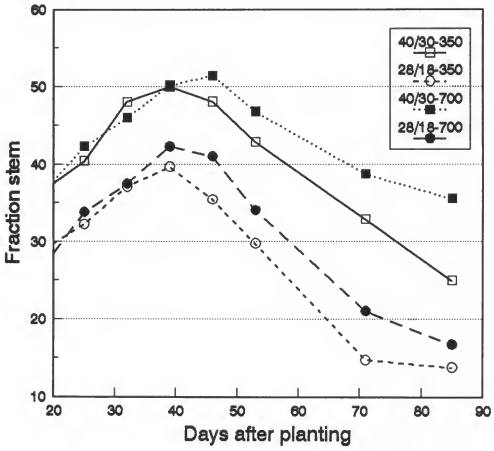


Figure 5-13. Effect of growth temperature and CO_2 treatments on seasonal course of fraction stem in 1994.

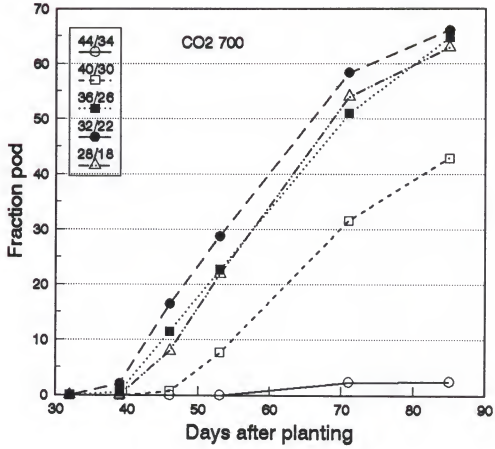


Figure 5-14. Effect of growth temperature on seasonal course of fraction pod at 700 μmol CO_2 mol^{-1} in 1994.

growing seeds, and prolonged reproductive development. Doubled CO_2 treatments had lower fraction pod than ambient CO_2 treatments (Figure 5-15). This is possibly associated with more carbohydrates stored in stems. The fraction pod is somewhat confounded with developmental differences caused by treatment temperatures. The 32/22 °C treatment, the optimum temperature for development, had the highest fraction pod on any given day after flowering. A partitioning principle that is widely accepted is that partitioning follows the order: (1) survival, (2) reproduction, (3) growth of existing organs, (4) increase in the number of organs and (5) storage of excess carbon for future use. According to the dry matter partitioning order, the larger stems and lower yield of elevated temperature treatments appeared associated with direct effect of temperature on seed growth rather than carbohydrate source limitation.

Both doubled CO_2 and elevated temperature significantly increased final plant height (Table 5-4), but there was no interaction between CO_2 and temperature on plant height. The taller plants were attributed to the longer development duration caused by elevated temperature and greater carbohydrate supply caused by doubled CO_2, and higher dry matter partitioning to the stems when seed growth was abnormal at high temperature.

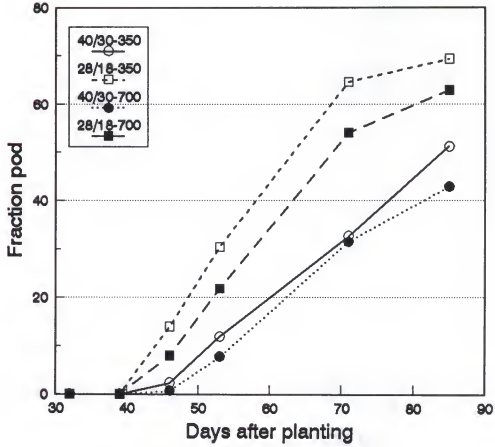


Figure 5-15. Effect of growth temperature and CO_2 treatments on seasonal course of fraction pod in 1994.

Seed Growth and Yield Projections

Seed growth

Single seed growth rate decreased as mean treatment temperature increased (Figure 5-16). The 28/18 °C treatments had the highest seed growth rates. Single seed growth rate was not affected by doubled CO_2. The effective filling period (EFP) of single seed increased as temperature increased, particularly above 32/22 °C (Table 5-4). The weight per seed decreased as treatment temperature increased (Figure 5-17). The 28/18 and 32/22 °C treatments had the highest seed size. The response of single seed growth rate and seed size to temperature is similar to the results of Egli and Wardlaw (1980). Elevated CO_2 did not increase the weight per seed. The seed size increased as seed growth rate increased, but size decreased as effective filling period increased. Swank et al. (1987) reported a similar trend among different soybean genotypes. The larger growth rate at 28/18 and 32/22 °C may be mainly due to larger cotyledon cell number (Egli et al., 1989). Baker et al. (1989) also reported that soybean seed size decreased as treatment temperature increased but it increased at doubled CO_2. However, CO_2 effect on seed size was not significant in this study.

Pod number increased as treatment temperature increased until 40/30 °C, and sharply decreased as temperature exceeded 40/30 °C (Figure 5-18). Doubled CO_2 increased the number of pods per plant but had no effect on seed size. Elevated

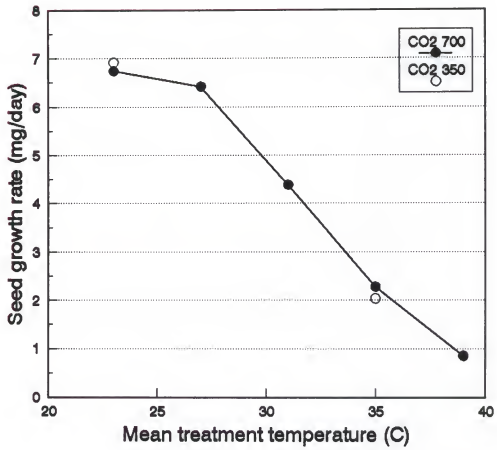


Figure 5-16. Effect of temperature and CO_2 treatments on seed growth rate in 1994.

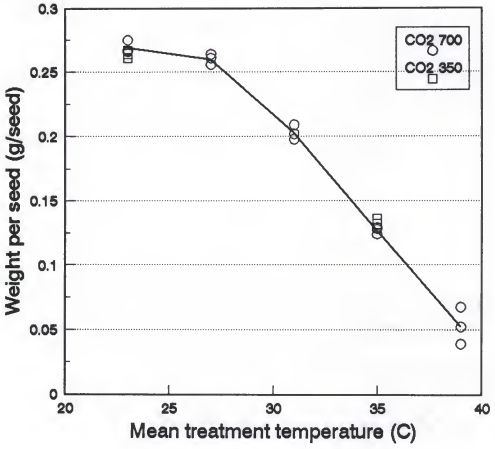


Figure 5-17. Effect of temperature and CO_2 treatments on weight per seed in 1994.

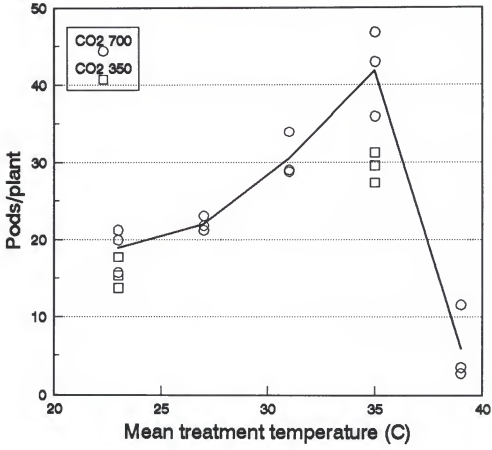


Figure 5-18. Effect of temperature and CO_2 treatments on the number of pods per plant in 1994.

temperature treatments up to 40/30 °C had higher pod number (and seed number) but smaller seeds. There was a quadratic relationship between the percentage of empty pods and treatment temperature (Figure 5-19). Elevated temperature caused more empty pods although elevated temperature increased pod number per plant up to 40/30 °C. Low temperature also caused more empty pods.

At 700 μmol mol^{-1} CO_2, soybean seed yield was highest at temperature from 27 to 31 °C (Figure 5-20). Somewhat lower yields at 23 and 27 °C are attributed to smaller canopy size and less light interception, and do not signify a problem with soybean growth processes. On the other hand, the yield decline at elevated temperature above 31 °C is important, because that decline results from decreased seed size and decreased single seed growth rate. As temperature increased, the number of seeds increased up to 40/30 °C, but the final seed size was decreased. Seed yield was increased 33% in 1993 and 31% in 1994 by doubled CO_2. Doubling CO_2 decreased the seed harvest index in both years, a phenomenon observed previously by Allen et al. (1991) and Baker et al. (1989). The final seed harvest index decreased with temperature in a same pattern to seed yield (Figure 5-21).

Soybean seed quality was decreased as temperature increased. As noted before, seed size was decreased as temperature increased. Above 27 °C mean temperature, there was a dramatic increase in percentage of shrunken seeds, which

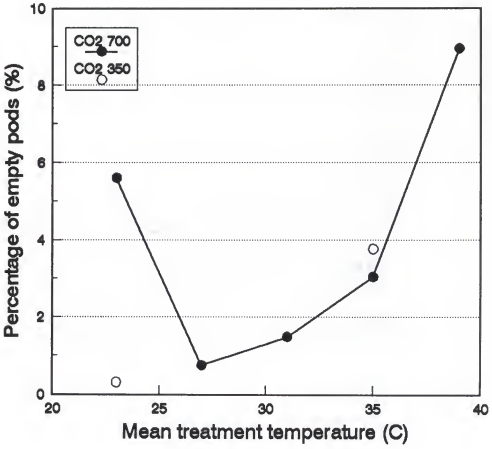


Figure 5-19. Effect of temperature and CO_2 treatments on percentage of empty pods in 1994.

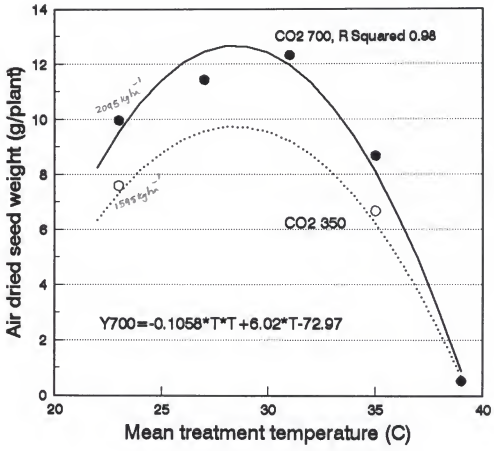


Figure 5-20. Effect of temperature and CO_2 treatments on seed yield (water content 10%) in 1994.

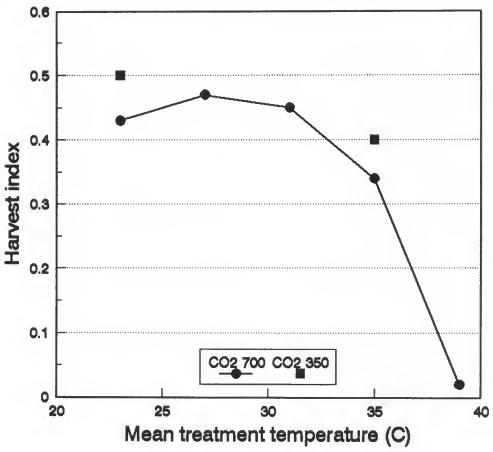


Figure 5-21. Effect of temperature and CO_2 treatments on seed harvest index in 1994.

reached 100% when mean treatment temperature was 35 °C or higher (Figure 5-22). Those shrunken seeds were of poor quality compared to seeds from the two cooler treatments.

Yield projections

CO_2 is projected to double and temperature is projected to increase 1.5 to 4.5 °C (IPCC, 1990). If CO_2 is assumed to be doubled, and air temperature (T) increases 2, 3, or 4 °C (ΔT), seed yield at doubled CO_2 can be calculated with equation from Figure 5-20, and seed yield at 700 μmol mol^{-1} CO_2 was found to be 30% higher than yield at 350 μmol mol^{-1} CO_2. Seed yield at ambient CO_2 can be computed by $Y_{350}=Y_{700}/1.3$, thus yield change can be calculated as:

$$[(Y_{700,\Delta T+T}-Y_{350,T})/Y_{350,T}]*100$$

Here $Y_{700,\Delta T+T}$ is the yield at doubled CO_2 and elevated air temperature and $Y_{350,T}$ is the yield at ambient CO_2 and current air temperature ranging from 26 to 34 °C. Seed yield change depends on the temperature change scenario (Table 5-5). The net change of seed yield includes the stimulation caused by elevated CO_2 and the decrease caused by a temperature elevation above a current mean temperature reference. The future soybean yield response to climate change will depend on current mean air temperature during soybean growth season and the degree of increase of air temperature. In current high temperature regions, yield decrease caused by elevated temperature is not compensated as much by doubled CO_2. If climate change really happens, northern cool areas where

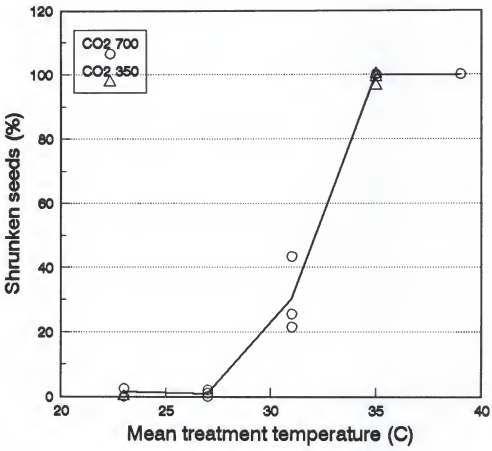


Figure 5-22. Effect of temperature and CO_2 treatments on percentage of shrunken seeds in 1994.

Table 5-5. Seed yield responses to a mean temperature increase from 2 to 4 °C at doubled CO_2 compared to current temperature and ambient CO_2.

Current Mean Temp.	Yield change		
	+2 °C	+3 °C	+4 °C
(°C)	---------- % ----------		
26	36.6	36.5	34.1
27	32.0	29.7	25.1
28	27.6	23.1	16.5
29	23.2	16.6	7.8
30	18.7	9.7	-1.5
31	13.7	2.1	-11.8
32	7.9	-6.8	-23.9
33	0.8	-17.7	-38.8
34	-8.3	-31.9	-58.3

current temperature is relatively low would benefit most. In temperate regions where current temperatures are mild, soybean seed yield could still be increased by doubled CO_2. For tropical area where current temperatures are relatively high, seed yield could be reduced.

Summary

Elevated temperature and doubled CO_2 increased leaf area by producing larger leaves, more branch leaves, and by increasing the total number of leaves on the main axis. Doubled CO_2 increased total dry matter by 55%, but different temperatures did not significantly affect total dry matter accumulation. Elevated temperature increased dry matter partitioning to stems and leaves late in the life cycle and resulted in larger plants. Doubled CO_2 significantly decreased

dry matter partitioning to leaves and pods, but increased dry matter partitioning to stems. Soybean development was not affected by doubled CO_2, however, the total growth duration was prolonged as the temperature increased from 28/18 to 44/34 °C. The increased growth duration was mainly from flowering to physiological maturity, and much less from planting to flowering. Elevated temperature increased the number of pods per plant up to 40/30 °C treatment, but decreased seed growth rate and weight per seed. Doubled CO_2 did not significantly affect seed growth rate or weight per seed but increased number of pods and seeds per plant. The optimum mean temperature for seed production was around 27-28 °C at doubled CO_2. The percentage of shrunken seeds was sharply increased as the mean treatment temperature increased above 27 °C. Harvest index decreased with doubled CO_2 and as temperature increased. Seed yield was increased about 30% by doubled CO_2 and decreased by temperature above 30 °C. If air temperature is increased and CO_2 concentration is doubled in the future, seed yield could be significantly increased in areas where the current air temperature is cool, and decreased in areas where current air temperature is high.

CHAPTER 6
COMPARISON BETWEEN SIMULATED AND OBSERVED SOYBEAN RESPONSES TO ELEVATED TEMPERATURE AT DOUBLED CO_2

Introduction

The crop production system is a complicated ecological system. Any single factor experiment can provide limited information from the system point of view. A multiple-factor experiment takes a lot of work and time to handle. Crop growth models, especially mechanistic crop growth models can evaluate the behavior of the multiple process system. The development and modification of crop models are therefore of importance in agricultural research.

Crop growth models have many potential uses, such as in research and crop production management (Boote et al., 1996). They can be used to test hypotheses, examine crop responses to particular ecological factor(s), and predict system behavior in research. Crop models have been using as a tool to forecast yield, optimize cropping systems and suggest crop climatic zoning. Crop models therefore have become valuable interdisciplinary research tools. They also can be effectively used by farmers as a guide in crop production when adaptations for a particular variety, soil, and modification of other parameters are made. Crop models are also used in day to day

operational management, such as irrigation and application of fertilizers. As the relationships between crop and ecological factors become more and more clear, crop models will be more and more robust for practical use in field production.

Several soybean growth models have been developed, such as SOYGRO (Jones et al., 1989), GLYCIM (Acock et al., 1993) and SOYMOD/OARDC (Meyer et al., 1979). SOYGRO is widely used in many countries. CROPGRO was developed on the basis of SOYGRO and two other legume (dry bean and peanut) growth models (Hoogenboom et al., 1992, 1993). The model predicts soybean growth behavior very well at ambient temperature. CROPGRO also describes soybean plant responses to variation in atmospheric CO_2 and temperature. However, as described in previous chapters, there are few reports of soybean physiological and growth responses to temperature higher than the ambient range at doubled CO_2.

The objective of this chapter is to compare simulation results from CROPGRO with observed data from the 1994 controlled-environment soybean experiment.

Materials and Methods

Model Overview

The 1996 release of CROPGRO was used for the simulations. This version had some code corrections compared to the 1994 release and had been calibrated to approximately 20 field data sets, of which seven were on the Bragg cultivar. CROPGRO

(Boote et al., 1996) consists of a main executable file that reads a crop management file, soil file, weather file, and three "genetic" files including species file, cultivar file and ecological-type file. FORTRAN language is used for the program. CROPGRO computes crop growth by considering crop carbon balance, soil nitrogen balance, and soil water balance. The carbon balance processes include carbon assimilation, respiration, carbohydrate partitioning to leaves, stems, pods and roots, carbon loss due to abscised parts, and growth or extension of different parts of the plants. A hedge-row light interception model is used to simulate crop photosynthesis. The hedge-row approach has better response to row spacing and planting density (Boote and Pickering, 1994). Therefore, the canopy photosynthesis simulated by hedge-row model is more accurate before the canopy is fully closed in comparison with that simulated on the basis of leaf area index. Crop development is dependent on temperature, photoperiod and water deficit. The development subroutine and corresponding crop species file allow use of different functions at different growth phases, such as temperature or daylength, before or after flowering. Users can easily change parameters when the model is used for a new species or variety.

The parameter differences due to cultivar are externally accessed through the cultivar data file, and management aspects such as planting date and density, irrigation, CO_2 concentrations are accessed through a crop management file.

Model Input

Weather data including daily photosynthetically active radiation from Gainesville, daily maximum and minimum temperature, and daily wind speed from the experimental treatments in 1994 were used as input. All the daily weather data are computed into hourly distribution by the model with a combined sine-exponential curve versus time of day. The time step of CROPGRO for photosynthesis, respiration and development is hourly.

The CROPGRO model was initially run unmodified, but crop development after flowering was not adequately simulated for above-normal temperatures. In order to compare crop carbon balance (dry matter accumulation and partitioning) over a correct life cycle, the CROPGRO model was rerun after modification of the development parameters. All other parameters were kept unchanged. The main variables such as canopy photosynthetic rate, leaf area growth, dry matter accumulation were therefore plotted against observed data. Further discussions are based on the simulated results after modification of the crop development (life cycle) parameters.

It should be pointed here that CROPGRO was developed on the basis of large amounts of field experimental data whereas the present soybean experiment (1994) was conducted in closed, sunlit, controlled-environment chambers. Dew point temperature for each chamber was controlled and was different from natural conditions. Although two layers of black shading were used to

drape the outside of chamber walls to reduce border effects, extra light was captured because the shade material was only brought up to 20 cm from the top of the canopy. The observed crop growth data might be expected to be somewhat greater than simulated output because of additional light capture. Therefore, the carbon accumulation data should mainly be used for qualitative comparison.

Results and Discussion

Development

The model predicted well the growth durations from emergence to first flower R1 (as described by Fehr et al., 1971) (Table 6-1), especially at moderate temperatures. However, the durations from emergence to physiological maturity R7 seemed over-predicted. The approach followed to modify the development was to:

-check the coefficients of ecological responses. Daylength sensitivity coefficient R1PRO was changed from 0.5 h. to 0.001 h. (less sensitive). The coefficient R1PRO describes the increase in daylength sensitivity after flowering.

-check VEGETATIVE DEVELOPMENT to adjust vegetative growth speed. In this case, the Tmax, highest temperature value, 45 °C was replaced by 48 °C.

-check EARLY REPRODUCTIVE DEVELOPMENT. Temperature optimum two was increased from 30 to 35 °C.

-check LATE REPRODUCTIVE DEVELOPMENT to modify the duration from R5 to R8. Original four-point temperature function (-48, 26, 35 and 45) was replaced by -48, 18, 22 and 55 °C respectively, to speed post-flowering development at cool temperatures and slow it at temperature above 22 °C.

-check the coefficients for number of genetic thermal days required for various phases from emergence to R8. For example, the parameter PH2-5, PHT-6 and PHT-8 values (19.5, 10, 15) were replaced by 22, 8, and 11 days respectively.

Parameters were repeatedly adjusted on the basis of the 1994 soybean experimental growth stage data. The model was run after the corresponding coefficients were adjusted. The simulated growth durations were then closer to observed ones (Table 6-1). However, being now mathematically correct does not necessarily mean this is statistically or biologically repeatable, it is important to check with other sets of observed data to confirm the modification of the parameters.

V stages as described by Fehr et al. (1971) were well predicted by CROPGRO at the temperatures lower than the 40/30 °C treatment and before 30 DAP (Table 6-2 and Figure 6-1). The leaf appearance rate calculated as the leaves at 31 DAP divided by 27 days from emergence to 31 DAP. The leaf appearance rate of the 44/34 °C treatment was observed to be similar to that of the 40/30 °C treatment; however, the model predicted slower development at 44/34 than 40/30 °C. Elevated temperature up to 44/34 °C did not significantly decrease the

Table 6-1. Comparison of simulated and observed reproductive phenology of soybean plants at doubled CO_2.

Temp. °C	Observed R1	Observed R7	Simulated* R1	Simulated* R7	Simulated# R1	Simulated# R7
	------days after planting------					
44/34	34	-	53	233	33	129
40/30	28	93	32	152	27	96
36/26	26	82	26	101	26	82
32/22	27	78	26	97	27	77
28/18	33✓	79	31	120	31	79

* without modification
\# after modification of developmental parameters

Table 6-2. Comparison of simulated and measured V stages (number of fully expanded main stem nodes) of soybean.

Temp-CO_2 °C-μmol mol^{-1}	Days after planting 17	24	31	38	45	52	70
	Simulated V stage						
44/34-700	1.7	3.3	4.9	6.5	8.2	9.5	9.5
40/30-700	3	5	7.1	9.2	9.2	9.2	9.2
36/26-700	3.1	5.3	7.5	8.7	8.7	8.7	8.7
32/22-700	2.6	4.6	6.5	8.2	8.2	8.2	8.2
28/18-700	1.7	3.2	4.8	6.4	7.3	7.3	7.3
40/30-350	3	4.9	6.9	8.9	8.9	8.9	8.9
28/18-350	1.7	3.2	4.8	6.4	7.3	7.3	7.3
	Measured V stages						
44/34-700	2.2	4.8	7	9.3	10.2	11.4	11.3
40/30-700	2.5	4.8	7.1	7.8	7.8	8.8	9.3
36/26-700	2.2	4.6	7	7.3	7.2	8.4	8.3
32/22-700	2.4	3.3	5.9	6.7	6.8	7.9	7.6
28/18-700	1	2.3	4.1	6.4	6.1	7.4	7.5
40/30-350	2.1	4.5	6.5	7.3	7.5	8.6	8.3
28/18-350	1.1	2.2	4.1	5.8	5.8	6.8	7.2

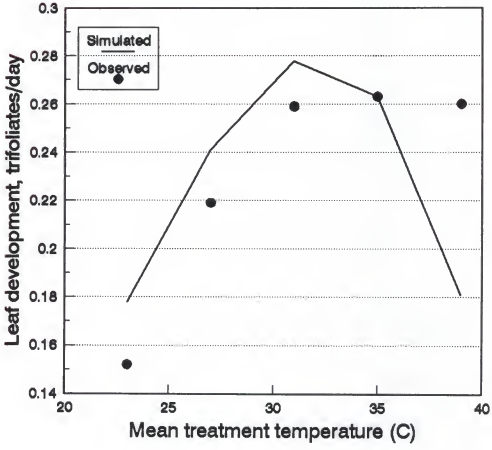


Figure 6-1. Comparison of simulated and observed leaf appearance rate of soybean between emergence and 31 DAP as affected by temperature at doubled CO_2.

leaf appearance rate before 31 DAP in comparison with 40/30 °C treatment, but it increased the observed final leaf number on the main stem because flowering was delayed. There was little difference between the predicted and observed final leaf number except the 44/34 °C treatment for which final leaf number was underestimated by two leaves (Figure 6-2). When parameter 45 °C was replaced by 55 °C in VEGETATIVE DEVELOPMENT section, simulated final leaf number (Modified) was closer to the measured values for 44/34 °C treatment.

Photosynthetic Rate and Leaf Growth

Simulated canopy gross photosynthetic rate at noon (Figure 6-3) was underestimated in comparison with observed values (Figure 6-4). Observed maximum canopy gross photosynthetic rate at noon was around 3 mg CO_2 m^{-2} s^{-1} and the rate remained high from 30 to 70 DAP under high light density. Simulated maximum photosynthetic rate at noon was about 1.8 mg CO_2 m^{-2} s^{-1}. The model underestimated gross photosynthetic rate at noon about 40%. In addition, the model over-predicted the noon photosynthetic rate of the 44/34 °C treatment after 70 DAP. Although growth duration was prolonged by the 44/34 °C high temperature, the leaves in the treatment were apparently not active for as long as the simulated crop. The difference between the simulated daily total gross photosynthesis (Figure 6-5) and observed values (Figure 6-6) had similar trends as canopy gross photosynthetic rate at noon.

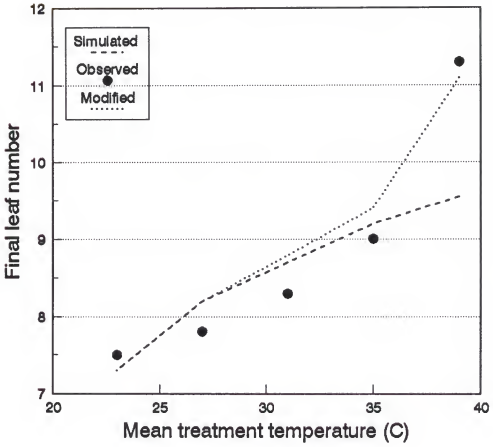


Figure 6-2. Comparison of simulated and observed final leaf number of soybean as affected by temperature at doubled CO_2.

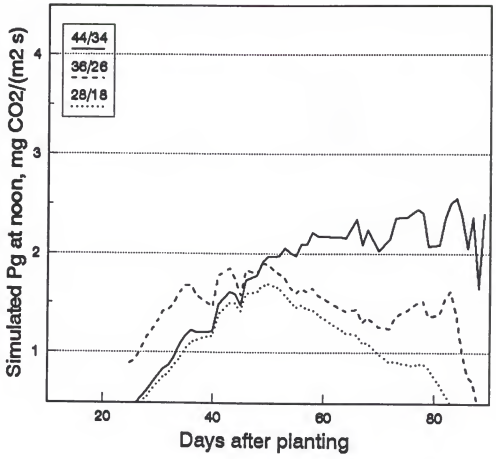


Figure 6-3. Simulated canopy gross photosynthetic rate of soybean at noon as affected by temperature at doubled CO_2.

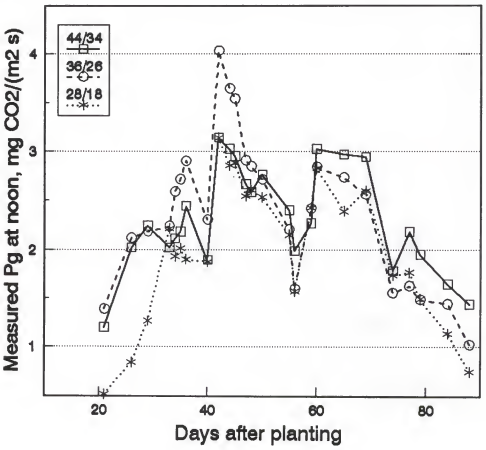


Figure 6-4. Observed canopy gross photosynthetic rate of soybean at noon as affected by temperature at doubled CO_2.

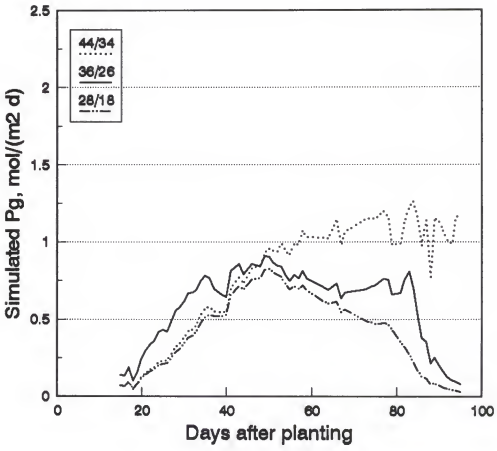


Figure 6-5. Simulated daily total canopy gross photosynthesis of soybean as affected by temperature at doubled CO_2.

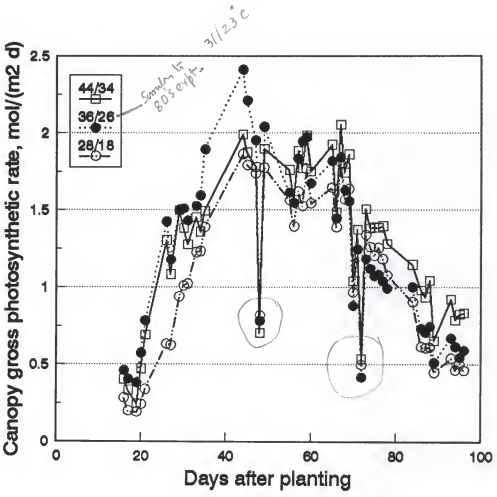


Figure 6-6. Observed daily total canopy gross photosynthesis of soybean as affected by temperature at doubled CO_2.

The underestimation of canopy gross photosynthesis may be related to some of the following PHOTOSYNTHETIC PARAMETERS AND light capture aspects:

-photosynthetic rate response to temperature.

-photosynthetic rate response to PAR

-photosynthetic rate response to CO_2

-more light coming from the border of the chamber

-respiration rate

-underestimated leaf area index

Leaf area index was underestimated about 20%, 40% and 30% for the 44/34, 36/26 and 28/18 °C treatments (Figure 6-7). Leaf area index and canopy photosynthetic rate interact. Low canopy photosynthetic rate may cause less new leaf growth, and low leaf area may also cause low canopy photosynthetic rate. Therefore, any parameter related to leaf growth also indirectly affects canopy gross photosynthetic rate. It may be necessary to check the coefficients related to both leaf growth and leaf/canopy photosynthetic rate. The potential modification approach to follow would include checking the following LEAF GROWTH PARAMETERS:

-rate of trifoliate leaf appearance versus temperature

-specific leaf area response to temperature

-leaf size

-time to termination of branch leaf area growth

-leaf senescence

The simulated leaf dry matter and observed values were

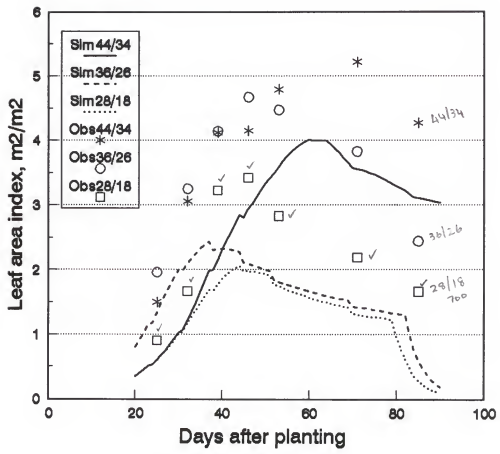


Figure 6-7. Comparison of simulated and observed leaf area index of soybean as affected by temperature at doubled CO_2.

reasonably close before 40 DAP (Figure 6-8). The underestimation of the 44/34 °C treatment was mainly due to the delay of leaf appearance rate in the simulation (Table 6-2). Of course, the underestimation of leaf dry matter is closely related to the estimation of photosynthetic rate. The model well predicted seasonal stem dry matter at 28/18 °C (Figure 6-9). However, the stem dry matter of the 44/34 °C treatment was significantly overestimated after 50 DAP. It appears that the dry matter partitioning rate to stem after 50 DAP is high and corresponding partitioning to leaf is low. It will be necessary to evaluate the dry matter partitioning rate to leaves and stems in addition to canopy photosynthetic rate, and comparing with experiment data.

Biomass and Yield

The model adequately predicted total above-ground dry matter for moderate temperature treatments (Figure 6-10). Dry matter of the 44/34 °C treatment was 60% overestimated at 110 DAP (date of last harvest). The final observed leaf number of the 44/34 °C treatment was 11.3, the leaves appeared senescent and the canopy photosynthetic rate decreased after 80 DAP. Although the 44/34 °C treatment had more branch leaves, total dry matter could not be as high as the simulated values because of the decreasing canopy photosynthetic rate after 80 DAP.

Pod dry matter was well predicted except that the 36/26

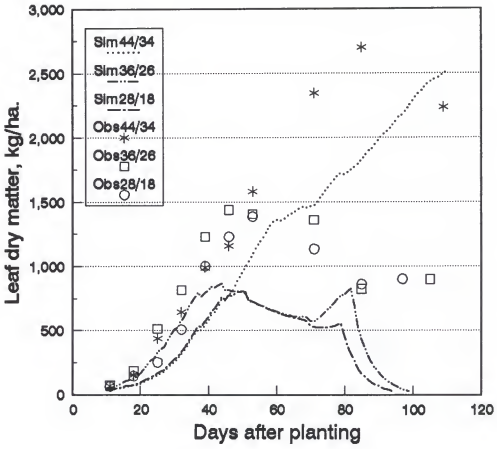


Figure 6-8. Comparison of simulated and observed leaf dry weight of soybean as affected by temperature at doubled CO_2.

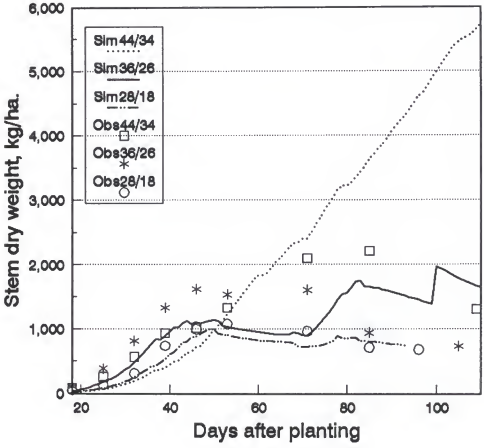


Figure 6-9. Comparison of simulated and observed stem dry weight of soybean as affected by temperature at doubled CO_2.

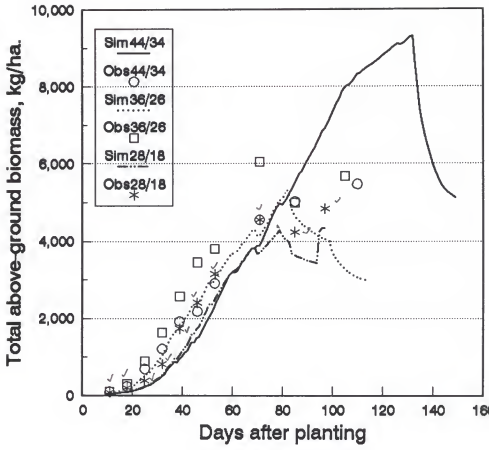


Figure 6-10. Comparison of simulated and observed total above-ground dry weight of soybean as affected by temperature at doubled CO_2.

°C treatment was slightly underestimated (Figure 6-11). Even at the elevated temperature 40/30 and 44/34 °C, CROPGRO correctly describes the dynamics of high temperature delay and reduction of pod dry matter accumulation. Final seed yields were also well predicted (Figure 6-12). The error at the 36/26 and 32/22 °C treatments was about 20% which might be systematically caused by the underestimation of pod dry matter prediction. The difference between the simulated and observed harvest index was small at elevated temperature (Figure 6-13), although the model overestimated harvest index somewhat at the 28/18 °C treatment. In this chamber experiment, many leaves of the 28/18 °C treatment were still green at the reproductive stage R7. Weight per seed was well predicted at the 40/30 and 44/34 °C treatments, but it was underestimated at temperatures lower than 36/26 °C (Figure 6-14). Larger weight per seed at the 28/18 and 32/22 °C were expected because low temperature reduced respiration and resulted in more carbohydrate availability and accumulation. The parameters which affect yield components are SEED AND SHELL GROWTH PARAMETERS. However, it should be the first priority to modify the vegetative growth. Reproductive modification should be conducted after reasonable vegetative growth simulation.

Summary

CROPGRO is a mechanistic crop growth model that was developed on the basis of large amounts of field experimental

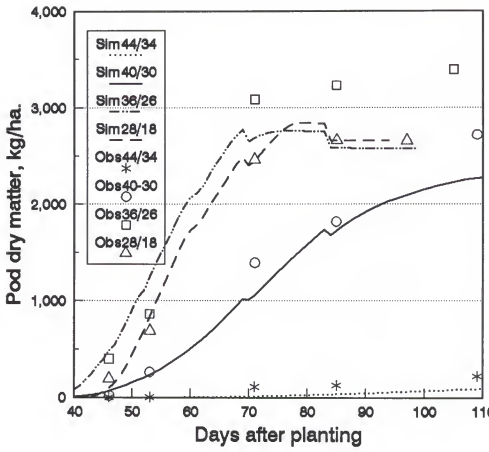


Figure 6-11. Comparison of simulated and observed pod dry weight of soybean over time as affected by temperature at doubled CO_2.

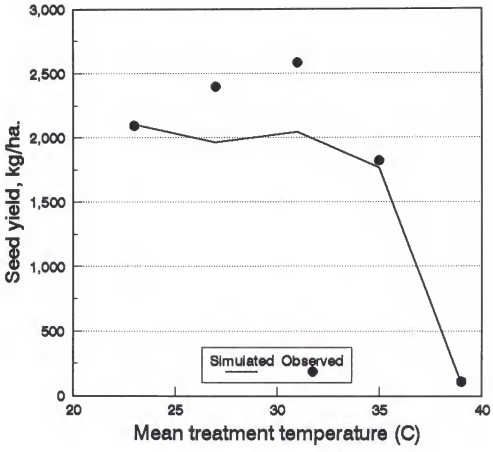


Figure 6-12. Comparison of simulated and observed final seed yield of soybean as affected by temperature at doubled CO_2.

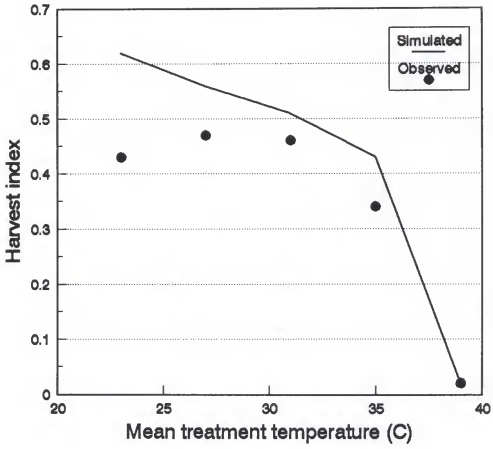


Figure 6-13. Comparison of simulated and observed harvest index of soybean as affected by temperature at doubled CO_2.

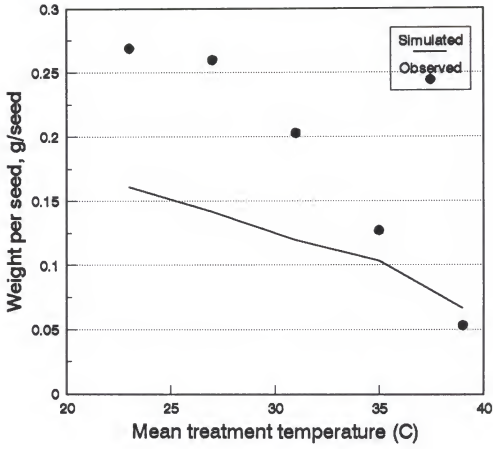


Figure 6-14. Comparison of simulated and observed weight per seed of soybean as affected by temperature at doubled CO_2.

data. The comparison between the simulated output and observed data showed that CROPGRO reasonably well predicted soybean growth and yield response to elevated temperature at doubled CO_2, but the experimental data comparisons also showed specific model areas that need improvements. Absolute growth and yield differences exist between predicted and observed, but are less worrisome because the experimental data may have an upward bias associated with insufficient bordering. CROPGRO can be used for the analysis of soybean response to climate change, and the model will be a powerful tool in crop system research and crop production if the parameter information for particular varieties and soils are available.

CHAPTER 7
CONCLUSIONS

The atmospheric CO_2 concentration and air temperature are projected to increase during the next century. Therefore, it is important to evaluate the effects of increased CO_2 and elevated temperature on soybean production. It was hypothesized that elevated temperature would have adverse effects on the reproductive growth of soybean on the basis of rice (Baker et al., 1992a, 1992b) and cotton (Reddy et al., 1991a, 1991b) response to elevated temperature. The objectives of this study were to evaluate the effects of doubled CO_2 and elevated temperature on soybean photosynthesis, respiration, evapotranspiration, growth and development, and yield responses. This chapter provides a brief summary and conclusions of this research.

Photosynthesis

Doubled CO_2 increased leaf photosynthesis from 25% to 50%, increased canopy photosynthesis 50% for the highest PAR at mid-day. The optimum temperature for photosynthesis at doubled CO_2 was between 35 to 40 °C. The temperature optimum for photosynthesis at doubled CO_2 was raised in comparison with that at ambient CO_2. Elevated temperature reduced leaf

photosynthetic rate during the vegetative growth phase, however, elevated temperature treatments had higher canopy photosynthetic rate during the reproductive phase because of larger leaf area index. The reasons may be, first, elevated temperature slowed down development speed and increased the final leaf number and area per leaf which caused larger leaf area index; second, elevated temperature caused fewer pods/seeds to set thereby making more carbohydrates available for leaf area growth; third, after the long term exposure to elevated temperature, the leaves might acclimate to elevated temperature. Downward acclimation of the leaf photosynthesis was observed in the experiment when soybean leaves grown under long term doubled CO_2 exposure were measured under ambient CO_2. The downward acclimation may be caused by lower rubisco protein. It was concluded that canopy photosynthesis will not be significantly affected by elevated temperature when grown at doubled CO_2 because elevated temperature increases leaf area index and doubled CO_2 raises the temperature optimum for photosynthesis.

Respiration

Whole plant dark respiration was compared versus days after planting for all treatments. Among the different treatments, the 36/26 °C treatment had the highest whole plant dark respiration (per unit land area) during the vegetative growth phase because this treatment had the highest canopy

photosynthetic rate and dry matter accumulation. The 44/34 °C treatment had the highest whole plant dark respiration during the reproductive growth phase. This was associated with the high leaf area index and the high gross photosynthesis of this treatment. Night time dark respiration was positively related to temperature and respiration substrate from day-time carbohydrate production. Doubled CO_2 treatment increased daily and seasonal whole plant dark respiration because doubled CO_2 increased photosynthesis and dry matter accumulation. Specific respiration (per unit dry matter) increased as the treatment temperature increased during the vegetative growth phase, but it was lowest for the 36/26 °C treatment during reproductive growth because this treatment had the largest dry matter accumulation. Doubled CO_2 increased specific respiration at 40/30 °C but decreased specific respiration at 28/18 °C. Specific respiration was directly affected by current temperature exposure and indirectly affected by long term temperature treatment which influenced plant development and nitrogen content. It was concluded that doubled CO_2 and elevated temperature increased the dark respiration but would not significantly affect dry matter accumulation because dark respiration was compensated by a higher carbohydrate production at doubled CO_2 and elevated temperature at which leaf area index increased.

Evapotranspiration

The difference of leaf-to-air temperature was negatively correlated to the vapor pressure deficit. Elevated temperature increased leaf temperature and vapor pressure deficit, therefore increasing canopy evapotranspiration (ET). Doubled CO_2 decreased ET by increasing canopy resistance to water vapor. Canopy resistance decreased as treatment temperature increased. ET is closely related to its driving force and stomata opening. The effect of doubled CO_2 on ET was significant at 28/18 °C, but not significant at 40/30 °C. Temperature is more important than CO_2 concentration in influencing ET of soybean plants. Doubled CO_2 significantly increased water use efficiency, but elevated temperature decreased water use efficiency. Elevated temperature increased ET and prolonged growth duration, and both elevated temperature and doubled CO_2 increased leaf area index which also resulted in higher ET. Although doubled CO_2 increased canopy resistance and reduced ET, the actual water requirement for soybean production would increase if atmospheric CO_2 concentration is doubled and air temperature also increases in the future.

Growth, Development and Yield Response

The optimum temperature for leaf area growth during the vegetative growth phase was 36/26 °C, whereas temperature lower or higher than 36/26 °C temperature reduced leaf area

growth. Elevated temperature and doubled CO_2 increased leaf area growth during the reproductive phase by producing more leaves on the main stem, larger area per leaf and more branch leaves. Specific leaf weight decreased as the treatment temperature increased up to 40/30 °C and increased with doubled CO_2. Doubled CO_2 increased total dry matter by 55%, but temperature did not significantly affect total dry matter accumulation. Growth duration from emergence to physiological maturity increased as the treatment temperature increased from 28/18 to 44/34 °C. The increase of growth durations was mainly from flowering to physiological maturity. Growth duration was not significantly affected by doubled CO_2. Elevated temperature and doubled CO_2 increased dry matter partitioning to stems during the reproductive phase and resulted in larger plants. Elevated temperature increased number of pods per plant up to 40/30 °C and pod number then decreased sharply as temperature increased further. Doubled CO_2 increased pod number per plant. Elevated temperature decreased seed growth rate and weight per seed, and increased percentage of shrunken seeds, but doubled CO_2 did not significantly affect seed growth rate, weight per seed and percentage of shrunken seeds. The optimum daily mean temperature for seed production was about 27/28 °C at doubled CO_2. Seed yield increased 30% at doubled CO_2 and decreased as treatment temperature increased above 28 °C. It was concluded that soybean seed yield will increase in current cool regions, and the seed yield and seed

quality would decrease in warm tropical regions if climate change happens. A potential strategy for climate change could be to shift the soybean production belt northward and to breed new varieties which can tolerate higher temperature.

Crop Growth Model CROPGRO

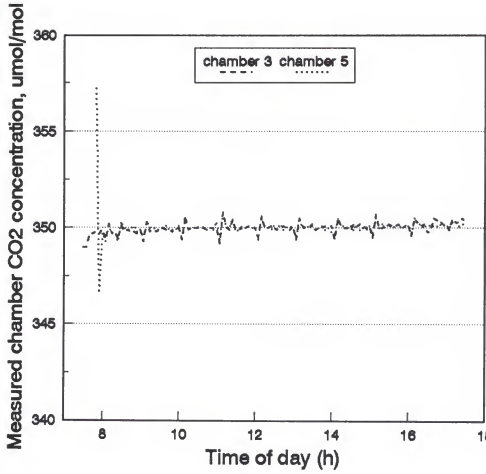
A comparison was made between the soybean growth data observed in the 1994 experiments and simulated results from the crop growth model CROPGRO. The results show that CROPGRO adequately predicted soybean growth and development responses to temperature at elevated CO_2. There were differences between the simulated results and observed data because of the extra light from the chamber border. With minor modification of model responses to temperature, CROPGRO will be a powerful model for crop system research and field production.

Further Research

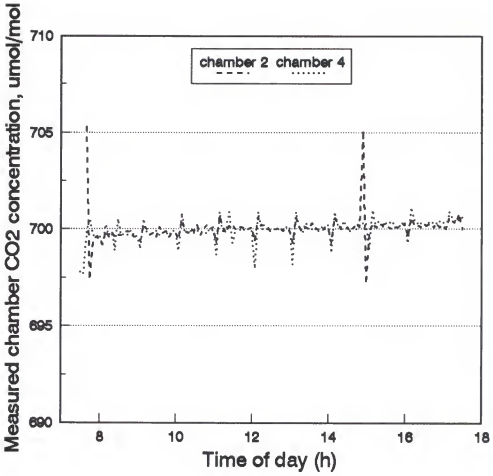
A significant finding in this experiment is that elevated temperature sharply reduces soybean seed yield. More experiments are necessary to know how elevated temperatures affect soybean seed yield and reproductive processes, such as pollination or fertility. It is still not fully clear how doubled CO_2 increases photosynthesis, more biochemical experiments are meaningful to know the mechanism. In future research, environmental factors such as dewpoint temperature should be controlled closer to natural conditions.

APPENDIXES

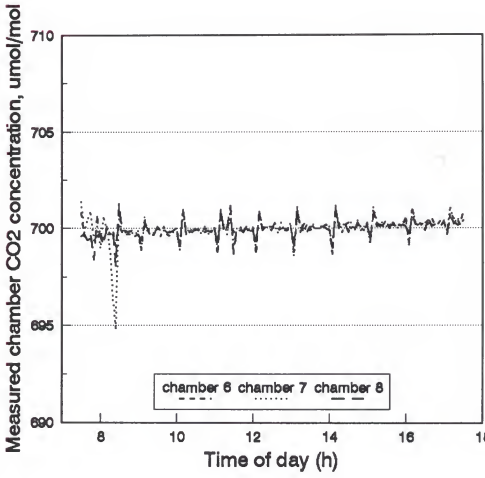
1. Measured CO_2 concentration in chambers 3 and 5 at 35 DAP in 1994.
2. Measured CO_2 concentration in chambers 2 and 4 at 35 DAP in 1994.
3. Measured CO_2 concentration in chambers 6, 7 and 8 at 35 DAP in 1994.
4. Measured chamber air temperature versus time of day in 1994.
5. Chamber air vapor pressure deficit versus time of day in 1994.



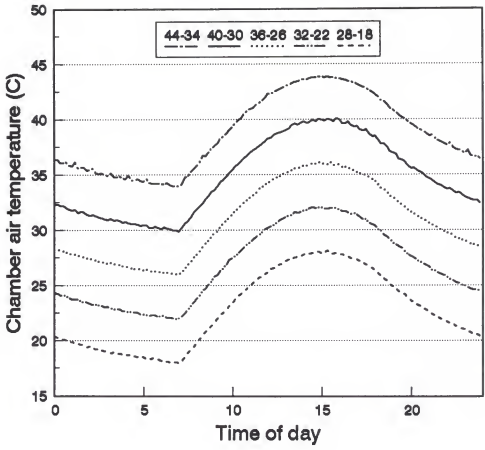
Appendix 1. Measured CO_2 concentration in chambers 3 and 5 at 35 DAP in 1994.



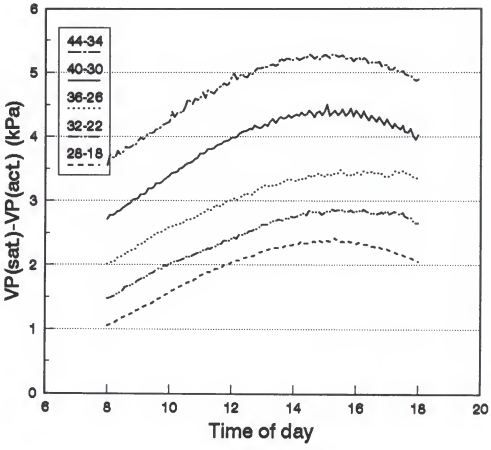
Appendix 2. Measured CO_2 concentration in chambers 2 and 4 at 35 DAP in 1994.



Appendix 3. Measured CO_2 concentration in chambers 6, 7 and 8 at 35 DAP in 1994.



Appendix 4. Measured air temperature versus time of day in 1994.



Appendix 5. Vapor pressure deficit versus time of day in 1994.

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BIOGRAPHICAL SKETCH

Deyun Pan was born on August 21, 1957. He grew up in Zhejiang Province, which is located in eastern and central China. He graduated from Zhejiang Agricultural University of China in July, 1982, with a B.S. degree in agronomy.

From August 1982 to August 1984 he participated in soil investigation work, and served as consultant for rice and vegetable production in Anji County Agricultural Bureau, Zhejiang, China. In September, 1984, he returned to Zhejiang Agriculture University for graduate study. He received an M.S. degree in crop ecology in July, 1987. Immediately after graduation, he was employed as a research associate, and one year later was conferred as an assistant professor at Zhejiang Agricultural University. From 1988 to 1992, he was research team leader for the project Simulation and System Analysis for Rice Production at the university. The project was funded by Zhejiang Education Foundation, the International Rice Research Institute, and the Center for Agricultural Research and Wageningen Agricultural University of the Netherlands.

Deyun came to the U.S. and started Ph.D. study at the University of Florida in June 1992. He hopes that he can make contributions to agriculture after his graduation.

I certify that I have read this study and that in my opinion it conforms to acceptable standards of scholarly presentation and is fully adequate, in scope and quality, as a dissertation for the degree of Doctor of Philosophy.

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